U.S. DEPARTMENT OF COMMERCE
National Technical Information Service

PB-280 051

Design and Evaluation of Laboratory Ecological System Studies

Oregon State Univ, Corvallis Dept of Fisheries and Wildlife

Prepared for

Environmental Research Lab, Duluth, Minn

Dec 77

PB 280 051

EPA-600/3-77-022
December 1977

Ecological Research Series

DESIGN AND EVALUATION OF LABORATORY ECOLOGICAL SYSTEM STUDIES

REPRODUCED BY
NATIONAL TECHNICAL
INFORMATION SERVICE
U. S. DEPARTMENT OF COMMERCE
SPRINGFIELD, VA. 22161

Environmental Research Laboratory
Office of Research and Development
U.S. Environmental Protection Agency
Duluth, Minnesota 55804

U.S. DEPARTMENT OF C
NAL TECHNICAL INFORM

INTEREST REPORT

TURN THIS FORM TO

FIELD)
ELD)

D

DISCLAIMER
☐ YES

RESEARCH REPORTING SERIES

Research reports of the Office of Research and Development, U.S. Environmental Protection Agency, have been grouped into nine series. These nine broad categories were established to facilitate further development and application of environmental technology. Elimination of traditional grouping was consciously planned to foster technology transfer and a maximum interface in related fields. The nine series are:

1. Environmental Health Effects Research
2. Environmental Protection Technology
3. Ecological Research
4. Environmental Monitoring
5. Socioeconomic Environmental Studies
6. Scientific and Technical Assessment Reports (STAR)
7. Interagency Energy-Environment Research and Development
8. "Special" Reports
9. Miscellaneous Reports

This report has been assigned to the ECOLOGICAL RESEARCH series. This series describes research on the effects of pollution on humans, plant and animal species, and materials. Problems are assessed for their long- and short-term influences. Investigations include formation, transport, and pathway studies to determine the fate of pollutants and their effects. This work provides the technical basis for setting standards to minimize undesirable changes in living organisms in the aquatic, terrestrial, and atmospheric environments.

This document is available to the public through the National Technical Information Service, Springfield, Virginia 22161.

TECHNICAL REPORT DATA

(Please read Instructions on the reverse before completing)

1. REPORT NO. EPA-600/3-77-022	2.	3. RECIPIENT'S ACCESSION NO. PB280051
4. TITLE AND SUBTITLE Design and Evaluation of Laboratory Ecological System Studies		5. REPORT DATE December 1977 (Issuing Date)
		6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S) Charles E. Warren and William J. Liss		8. PERFORMING ORGANIZATION REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS Department of Fisheries and Wildlife Oak Creek Laboratory of Biology Oregon State University Corvallis, Oregon 97331		10. PROGRAM ELEMENT NO. 1BA608
		11. CONTRACT/GRANT NO. Grant No. R802286
12. SPONSORING AGENCY NAME AND ADDRESS Environmental Research Laboratory--Duluth, MN Office of Research and Development U.S. Environmental Protection Agency Duluth, Minnesota 55804		13. TYPE OF REPORT AND PERIOD COVERED
		14. SPONSORING AGENCY CODE EPA-600/03

15. SUPPLEMENTARY NOTES

16. ABSTRACT

Design and evaluation of laboratory ecological system studies are considered in relation to problems and objectives in environmental toxicology. Ecological systems are defined to be organismic systems together with their level-specific, co-extensive environmental systems and to occur at individual, population, and multispecies levels of biological organization. So that the basis for judgments on the relevance and adequacy of laboratory ecological system studies for solution of problems in environmental toxicology will be clear, a conceptual framework defining with abstract generalizations the nature of biological systems is presented and employed. And a graphical calculus is used to deduce isocline systems and dynamic as well as steady-state behaviors of multispecies systems, so as to illustrate the importance of empirical evaluation of the capacities, not simply the performances, of laboratory ecological systems. Within the context of apparent toxicological problems and this conceptual framework, the relevance and adequacy of laboratory ecological system studies on toxicant effects and behaviors are evaluated.

17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS		b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group
models	toxicology	laboratory	06 C,F,T
environment simulation		microcosms	14 B
closed ecological systems			
aquatic biology			
communities			
populations			
pollution			

18. DISTRIBUTION STATEMENT RELEASE TO PUBLIC	19. SECURITY CLASS *(This Report)* UNCLASSIFIED	21. NO. OF PAGES 129
	20. SECURITY CLASS *(This page)* UNCLASSIFIED	22. PRICE A07 - A01

EPA Form 2220-1 (9-73)

☆ U.S. GOVERNMENT PRINTING OFFICE 1978— 757-140/6672

EPA-600/3-77-022
December 1977

DESIGN AND EVALUATION OF LABORATORY ECOLOGICAL SYSTEM STUDIES

by

Charles E. Warren and William J. Liss
Department of Fisheries and Wildlife
Oak Creek Laboratory of Biology
Oregon State University
Corvallis, Oregon 97331

Grant No. R802286

Project Officer

John Eaton
Chemical Pollutant Section
Environmental Research Laboratory
Duluth, Minnesota 55804

ENVIRONMENTAL RESEARCH LABORATORY
OFFICE OF RESEARCH AND DEVELOPMENT
U.S. ENVIRONMENTAL PROTECTION AGENCY
DULUTH, MINNESOTA 55804

1a

DISCLAIMER

This report has been reviewed by the Environmental Research Laboratory, Duluth, U.S. Environmental Protection Agency, and approved for publication. Approval does not signify that the contents necessarily reflect the views and policies of the U.S. Environmental Protection Agency, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

FOREWORD

Our nation's freshwaters are vital for all animals and plants, yet our diverse uses of water---for recreation, food, energy, transportation, and industry---physically and chemically alter lakes, rivers, and streams. Such alterations threaten terrestrial organisms, as well as those living in water. The Environmental Research Laboratory in Duluth, Minnesota develops methods, conducts laboratory and field studies, and extrapolates research findings

--to determine how physical and chemical pollution affects aquatic life

--to assess the effects of ecosystems on pollutants

--to predict effects of pollutants on large lakes through use of models

--to measure bioaccumulation of pollutants in aquatic organisms that are consumed by other animals, including man

This report presents a carefully reasoned analysis of the character of ecosystems as a basis for designing more meaningful, relevant and useful field and laboratory studies of ecological processes. The potential would seem to be great for utilizing theoretical frameworks with the breadth of those presented here to bridge the gap between traditional, overly-simplified laboratory investigations and responses of intact natural systems.

Donald I. Mount
Director
Environmental Research Laboratory
Duluth, Minnesota

ABSTRACT

Design and evaluation of laboratory ecological system studies are considered in relation to problems and objectives in environmental toxicology. Ecological systems are defined to be organismic systems together with their level-specific, co-extensive environmental systems and to occur at individual, population, and multispecies levels of biological organization. So that the basis for judgments on the relevance and adequacy of laboratory ecological system studies for solution of problems in environmental toxicology will be clear, a conceptual framework defining with abstract generalizations the nature of biological systems is presented and employed. And a graphical calculus is used to deduce isocline systems and dynamic as well as steady-state behaviors of multispecies systems, so as to illustrate the importance of empirical evaluation of the capacities, not simply the performances, of laboratory ecological systems. Within the context of apparent toxicological problems and this conceptual framework, the relevance and adequacy of laboratory ecological system studies on toxicant effects and behaviors are evaluated.

CONTENTS

Foreword iii
Abstract iv
Figures vi
Tables x
Conclusions and Recommendations 1

I Problems, Objectives, Methods and Explanation in Environmental Toxicology 5
II Conceptual Considerations in Environmental Toxicology 13
III Theoretical Considerations in Environmental Toxicology . . . 29
IV Empirical Considerations in Environmental Toxicology 56
V Conceptual, Theoretical, and Empirical Efforts to Resolve Problems in Environmental Toxicology 92

References 112

FIGURES

Number		Page
1	The conceptual continuum of levels of explanation and understanding of an individual scientist. This is considered to be within the context of the scientific community. After Warren, Allen, and Haefner (MS).	11
2	A biological system viewed throughout its existence as being composed of an organismic system together with its spatially and temporally co-extensive environmental system. After Warren, Allen, and Haefner (MS).	15
3	A diagrammatic view of an organismic system showing that from some potential capacity the organismic system passes through a particular sequence of realized capacities jointly determined by its potential capacity and the actually prevailing environmental system. After Warren, Allen, and Haefner (MS) .	17
4	Organismic subsystems and their level-specific environments, all of which are incorporated by an organismic system having its own particular environment. After Warren, Allen, and Haefner (MS)	18
5	Kinetic diagrams representing defined multispecies system, including plants (P), herbivores (H), and carnivores (C). Rate of light input (I) and rate of exploitation (E) represent external environmental variables. Light intensity (R) is a variable dependent on I and P. Competition, commensalism, and mutualism are represented in B. And a toxicant (T) directly affecting only carnivore C is represented in C.	34
6	Phase planes and interrelated isocline systems representing a sequence of predator-prey interactions in a simple community. .	37
7	Derivation of prey isoclines on the C-H phase plane by graphical summation of herbivore gain and loss response functions. . . .	39
8	Derivation of the herbivore production gain response functions used in constructing the prey isoclines on the C-H phase plane.	41
9	Derivation of predator isoclines on the C-H phase plane by graphical summation of carnivore gain and loss curves.	45

Number Page

10 Derivation of the carnivore production gain response functions used in constructing the predator isoclines on the C-H phase plane. 47

11 (A) Direct effects of toxicant T on the relative growth rate of carnivore C in relation to herbivore H biomasses, at concentrations of 0T, 1T, and 2T. (B) Direct effects of toxicant on the loss or mortality rate of carnivore C are shown to occur at 2T but not at 0T and 1T and are taken to be linearly proportional to biomass of C. 49

12 Possible steady-states (indicated by circles, squares, and triangles) and trajectories of biomasses of carnivore C, herbivore H, and plant P population and light intensity R under different rates of light input (low I, medium I, and high I) and different levels of fishing effort E, when toxicant T is absent and when it is present at concentrations of 1T and 2T. 50

13 Steady-state biomass isopleths of the alga *Chlamydomonas reinhardtii* (A and B) and the protozoan *Tetrahymena vorax* (C and D), under different light and flow regimes when nitrate concentration was 0.5 mM (A and C) and when it was 0.05 mM (B and D) in continuous flow cultures. These diagrams illustrate population scopes for performance in terms of steady-state biomasses and environmental variables. After Taub (1973). 53

14 Effects of the addition of 0.2, 2, and 20 ppm Aroclor 1242 on the growth of *Chlamydomonas reinhardtii*. Each point represents the mean of two observations whose individual values are indicated as the range. After Morgan (1972). . . . 68

15 Diagrammatic representation of theoretical and empirical partial evaluation of capacities of laboratory ecological systems by determination of scopes for performance as sets of performances under different environmental conditions. . . . 73

16 The influences of a controlling factor such as temperature (A), lethal levels of the controlling factor (B), a limiting factor such as dissolved oxygen (C), and the cost of additional physiological regulation as might be caused by a toxicant (D) on the active and standard metabolic rates and on the metabolic scope for performance of a hypothetical poikilothermic animal such as a fish. After Fry (1947). 75

17 Theoretical effects of temperature change on the food consumption, energy budget, and scope for growth performance of a hypothetical poikilothermic animal having food available in different amounts. After Warren (1971). 76

Number Page

18 Relationships between median survival time of rainbow trout and concentration of zinc ion in water having different total hardness. After Lloyd (1960). 77

19 Percentage isopleths representing scope for survival of the fourth zoeal stage of larvae of the crab *Sesarma cinereum* in relation to temperature and salinity of water. After Maguire (1973). 79

20 A three-dimensional diagram showing the influence of both oxygen concentration and water velocity on the mean dry weights of newly hatched coho salmon fry developing from embryos reared throughout development at the various combinations of oxygen concentration and water velocity represented by the intersection of the curves. After Shumway, Warren, and Doudoroff (1964). 80

21 Relationships between rates of food consumption and growth of groups of steelhead trout kept at different fluctuating temperatures in a spring experiment. Rates of food consumption and growth are expressed in dry weights. The initial mean wet weight of the fish was 2.29 g. Numbers in parentheses indicate the number of fish which died in a treatment. After Wurtsbaugh (1973). 81

22 Energy budgets showing relationships between food consumption rate, energy and material uses and losses, and dissolved oxygen concentration for juvenile coho salmon in laboratory studies at 15C in the summer. The influence of both food availability and oxygen concentration on scope for growth are apparent in differences in growth parts of these budgets. After Thatcher (1975). 82

23 The finite rate of increase (λ) as a function of temperature and moisture for the grain beetles, *Calandra oryzae* and *Rhizopertha dominica* living in wheat. Rates of increase are indicated by contour lines that describe conditions with identical values of λ. After Andrewartha and Birch (1954). 83

24 Curves indicating relation of yield of guppies per 3-week brood interval to biomass and exploitation rate (indicated percentages) at each diet level. Points indicated for 0 percent exploitation rate are average population levels for the 3 weeks immediately berore exploitation. After Silliman (1968). 84

Number Page

25 Approximations of biomass-production curves for cutthroat trout in the laboratory stream ecosystems having five different basic capacities to support trout production in the spring 1968 experiment. After Warren (1971). 86

26 Relationships between food consumption and growth of juvenile chinook salmon at different concentrations of kraft process pulp and paper mill effluent, when the fish were fed controlled rations in aquaria (A). And (B) relationships between the biomass of juvenile chinook salmon and their production in laboratory streams receiving similar effluent and in streams not receiving such effluent. After Tokar (1968) and Seim et al. (1977) 87

27 Relationships between the growth rate of sculpins and the density or biomass of the insects upon which they fed in laboratory streams into which different concentrations of dieldrin were introduced (A). And (B) relationships between the biomass of sculpins and their production in the same streams. After Warren (1971). 88

28 Delineation of human goals, problems, institutions, and institutional objectives and approaches. 97

29 Delineation of the goals, problems, objectives, and approaches of man's scientific institution. 98

30 Problems, objectives, and methods of laboratory ecosystem studies in relation to those of other studies. 100

31 Apparent and possible objectives of laboratory ecosystem studies in environmental toxicology. 101

TABLES

Number		Page
1	Ecological magnification indices (concentration of chemican in organism/concentration of chemical in water) obtained from laboratory multispecies systems having different designs and experimental protocols.	71

CONCLUSIONS AND RECOMMENDATIONS

1. In the creation and utilization of environments to satisfy human needs and aspirations, resource, cultural, political and technological problems are perceived. The introduction of massive amounts of toxic substances for pest control and as a result of industrial and other processes has led to the development of such problems. Solutions of these and other problems having social dimensions are sought through the legislative, judicial, administrative, educational, technological, and scientific institutions societies develop. This report deals primarily with scientific approaches--particularly laboratory ecological system studies--to problems associated with effects, transport, accumulation, and degradation of toxic substances. But the context of use and success of scientific approaches is the entire complex of social institutions, so that not only the limitations of science but also the limitations of other institutions are involved.

2. The problems with which this report is primarily concerned are: accumulation of toxic substances in biological products utilized by man; reductions in production and yield of biological resources caused by toxic substances; and toxic alteration of the capacity, structure, and persistence of ecological systems of importance to man. And the objectives of laboratory ecological system studies with which we deal are taken to be: assay of the relative toxicity of toxic substances; determination of the behavior of toxic substances; and determination of the effects of toxic substances on individual organisms, biological populations, and biological communities.

3. Science generally recognizes that its methods must be evaluated against the objectives they are intended to accomplish, but it is not so generally recognized that the objectives of science ought to be evaluated against problems of understanding or more concrete problems of life. The difficulty of evaluating objectives against problems, and even methods against objectives, is that different people perceive problems and even understand stated objectives differently. This is a natural outcome of differences in conceptual structures within which people understand their experiences. Such differences lead to difficulties in all human institutions, including science. Disagreement ensues as to what the problems really are, what objectives ought to be, and how these are to be approached. Disagreement in itself is not undesirable but it cannot be dealt with rationally unless its bases are explicated.

4. Rationality can be taken to be that which makes understanding possible. Since Immanuel Kant, philosophers of science have recognized that any understanding whatsoever depends on *a priori* conceptual constructs. But these constructs are not usually specified, even in science, at any higher level than formal theory. Were they to be, understanding, and thus rationality, would more generally be possible, even when there are disagreements over assumptions and conclusions. We take what we will call a *conceptual framework* to be a description of some domain of human experience, together with rules for its use. Specification of such conceptual frameworks is needed in all human institutions including science, for they would serve as an important aid in communication, problem perception, and evaluation of the adequacy of approaches to problems.

5. In this report we review a conceptual framework developed for biology. It consists of a set of four abstract generalizations articulated in natural language, together with conceptual and procedural rules. The generalizations define a biological system, at any level of organization, as an organismic system together with its level-specific co-extensive environmental system, through all states of the organismic system from its origin to its end. We believe this to be necessary for adequate explanation of biological systems. Organismic systems exhibit *performances* like organization, structure, replication, and persistence. To exhibit such performances, organismic systems must have the *capacities* to do so. Performances are determined by capacities interacting with environments. Thus, so long as environments are changing, as in nature they must, performances are likely to change, and no particular time-variant or steady-state performance is of much interest. It is the capacity of the organismic system that is of interest, and theoretical and empirical approaches ought to be designed to make partial evaluation of capacities possible--no full evaluation of a theoretical concept such as capacity being possible.

6. Conceptual frameworks, in the very general way in which they describe whole domains, do not provide the particular explanations of particular systems that we need. For this, theories as abstract scientific deductive systems leading to theorems that can be translated into empirical generalizations are needed. Particular empirical generalizations alone do not account adequately for human observational experience. A universal theory allows us to deduce many different empirical generalizations and so explain and logically unify them. In so doing, theory makes more clear the boundary conditions of empirical generalizations, which is very important in any applied science such as environmental toxicology. But because of its greater particularity, a theory leaves out much of what must be involved in natural and social systems, this making conceptual frameworks as well as theories necessary in human understanding and solution of problems.

7. For defined organismic systems, we illustrate that changes in the number and levels of environmental factors, including toxicants, change not only the time-variant behavior of the systems and their parts but also their steady-states. No particular observation of a behavior that is time-variant or even in steady state is of much interest. Rather, it is the domain of possible time-variant behaviors and steady states under ranges of environmental

factors that is of more general interest and greater value in application to solution of problems in environmental toxicology. With changes in process and structure of organismic systems on any level of biological organization, changes in the effects, transport, accumulation, and degradation of toxic substances are to be expected. Thus any particular measurement of these may not be of much value in application to natural systems and the solution of problems occurring there.

8. Organismic systems can be defined as occurring at individual organism, population, and community levels of biological organization. Laboratory models of ecological systems can be created at the individual level, the population level, and sometimes at multispecies levels, but probably not at the level of the biological community. Individual organisms, because of evolution, reproduction, and development, are natural organismic systems having their species-specific natural capacities. Populations developing in the laboratory through the reproduction, development, growth, and survival of individual organisms may have capacities resembling those of natural populations of the same species, but these capacities are likely to be influenced by laboratory environmental conditions. Multispecies systems created in the laboratory generally do not have capacities of natural multispecies systems. This is because in bringing together different species having their own capacities, we create in the laboratory higher level systems having capacities in part determined by our own actions. It is not clear to us that multispecies systems having capacities for organization, structure, and persistence have usually been created in the laboratory. But even when they may have been, it is difficult to know what if any natural level of biological organization has been modeled, unless some carefully studied natural multispecies system has been recreated in the laboratory. This has not often been done. Whatever is created in the laboratory, it must generally be at a much lower level of organization than a biological community, which together with its environment forms what is usually called an ecosystem. And we ought not to attribute directly to natural ecosystems performance and capacity evaluations based on model ecosystems. This applies to any sort of evaluation of the effects or behaviors of toxic substances.

9. Individual organisms, because of their naturally endowed capacities, can generally be more meaningfully evaluated in the laboratory than can higher levels of organization. Moreover, it is generally more practical to evaluate these capacities through determination of *scope for performance* over a range of kinds and levels of environmental factors. This applies to effects and behaviors of toxicants, as well as to other environmental factors. Such evaluations are most valuable if the entire life history of the individual organism is taken into account.

10. Development of a laboratory population, as a higher level system, requires provision of environmental conditions suitable for completion of individual life histories and persistence of the developing population through several generations. Creation and study of population systems in the laboratory is practical only for small organisms having relatively short life histories. When it is accomplished, the performances and

capacities of laboratory populations should be evaluated over as wide a range of kinds and levels of environmental conditions as possible, especially if results with toxicants and other environmental factors are intended for application to solution of problems occurring in nature.

11. Multispecies systems having their own level-specific capacities are very difficult to develop in the laboratory. This requires not only the provision of conditions suitable for life history completion and individual population persistence but also that the populations are so adapted one to another as to form a multispecies system that as a whole has the capacity to persist under provided environmental conditions. This has rarely been done for systems of more than two species of small organisms. And even if such systems are successfully created, it is not any particular time-variant or steady-state performance that has much meaning. Their domains of time-variant behaviors and steady states should be evaluated, even if only partially, by study of the system under as wide a range of kinds and levels of environmental factors as possible. This is important if we are interested in effects, transport, accumulation, and degradation of toxic substances, because these will all change as functions of system process and structure. Some problems may best be approached by means of multispecies laboratory systems. But, if this is the intention, there must be a commitment to the exceedingly difficult and long-term process of creating and studying such systems. Anything less is not likely to be worthwhile and may be very misleading.

12. Not only the perception of problems but also the different interpretations given even defined objectives demand some specification of the conceptual structures on which these are based, if our search for solutions to problems in environmental toxicology is to be made understandable and thus rational. Moreover, the design and interpretation of the sorts of experimental studies of ecological systems considered here are dependent on presuppositions, whether or not these are specified. But without development and specification of conceptual frameworks and theories, the design of experiments and the meaning of their results can hardly be evaluated, at least in a rational way that can be communicated to all concerned. And finally, ways of applying results to nature for the solutions of problems in environmental toxicology are never implicit in the experimental results themselves, because the systems on which these were determined are much too different from nature. Here again, and for all these reasons, conceptual frameworks and theories are needed. Far more effort in environmental toxicology should be devoted to the development of adequate conceptual frameworks and theories than has been in the past. Understanding and solution of our problems with toxic substances can never be based on empirical investigation alone.

I. PROBLEMS, OBJECTIVES, METHODS, AND EXPLANATION IN ENVIRONMENTAL TOXICOLOGY

A. PROBLEMS AND OBJECTIVES IN ENVIRONMENTAL TOXICOLOGY

Any consideration of the design and evaluation of laboratory ecosystem studies in environmental toxicology should deal with social-technological problems as well as with objectives and methods of research intended to be useful in the reduction of these problems. For the apparent relevance of objectives and the adequacy of methods in environmental toxicology depends very much of the nature of the problems, or, more precisely, on how we perceive these problems. Those of us interested in environmental toxicology know something about problems associated with the use of toxic materials. And we are aware that the solution of such problems demands socio-economic and technological knowledge and action that would best be based on scientific understanding. But we are also aware that social solutions may need to be attempted, and very often are, in the absence of adequate understanding. In consequence, continued and uncontrolled use of some very hazardous materials may be permitted. And severe restrictions may unnecessarily be placed on the use of other materials having considerable potential value to man.

But in all this, there is very often sincere disagreement among individuals and groups as to just what the problems really are and whether or not the uses of particular toxic materials present unacceptable hazards. Differences in the interests and knowledge of people inevitably lead to differences in problem perception. The occurrence of differences in problem perception and the social and scientific difficulties to which this leads should, at the outset, be clearly recognized. We are dealing with social and natural problems that are probably of irreducible complexity, and there is certainly much to justify different opinions. Differences of opinion, in themselves, are not bad and indeed may lead to elucidation of different aspects of complex social and natural systems. But rational consideration of differences of opinion is only possible if their conceptual and observational bases are made known, and this is rarely done. The need for social action, the relevance of scientific objectives, and the adequacy of scientific methods then become matters in environmental toxicology that are very difficult to evaluate.

The problems with which we will here be concerned result from the introduction of relatively large amounts of toxic materials into the environment; we will not consider problems of drug toxicity or occupational health. Problems associated with pesticide use in agriculture and forestry prompted preparation of this report, but most of the ensuing discussion pertains as much to toxicants in industrial effluents. Along with benefits deriving from the use of pesticides, there are many side effects, not all of which are known but many of which have undesirable environmental effects and may be quite hazardous to man himself. Reduction or loss of natural populations, alteration in the structure of biological communities, decreased production and yields of exploited wild populations, and the accumulation of substances hazardous to man are among the problems that concern us. The biological systems as well as the social systems within which such problems are perceived to occur are almost unknowably complex.

They extend from physiological levels of organization to biological community levels and even beyond. Here, we will mainly address ourselves to scientific approaches dealing with individual organism, population, and higher levels of biological organization.

We take the ultimate goal of science to be the continuous advance of human understanding. Science does this through conceptual frameworks and theoretical and empirical explanations. And explanation, so as to achieve more understanding of phenomena in environmental toxicology, ought to be the primary objective of investigation of toxic materials. But understanding of complex biological systems will ever be very partial, and scientists, recognizing this, generally have very limited objectives: assay of the relative toxicity of different materials, determining their behavior in biological systems, and determining some of their effects on individual organisms, populations, and perhaps even biological communities. So as not to appear naive, we often claim for our approaches to such objectives only that they are bioassay techniques, or other ways of establishing environmental standards, or screening techniques, or simple models to give us at least some initial understanding. But in so doing, we ought not to delude ourselves that our findings thus need not relate to problems in complex natural and social systems. For it is to these systems that the results will be applied. A simple laboratory technique for screening for approval of use of toxic materials that does not account for natural complexity may lead to approval of a hazardous material, or needlessly prevent the use of some potentially valuable one.

Thus our objectives as well as our methods need our continuous evaluation. Scientists generally recognize that evaluation of their methods is always legitimate but they may resist evaluation of their objectives, this seeming to infringe upon scientific freedom. We can accept the need for a diversity of objectives in any vigorous science and still recognize that all objectives are not likely to be equally relevant or worthwhile to the pursuit of solution of particular problems. Objectives, in our opinion, should be scrutinized in view of the nature of the problems to which they are claimed to pertain. This is no simple matter, because so doing requires that we have some at least initially adequate notion of the nature of the biological system in which a problem appears to occur. A major section of this report will be devoted to consideration of the nature of biological systems, in part to facilitate evaluation of objectives.

Science might be described as the art of defining problems in ways that they can be solved. The greatest advances in physics have been based on this. Still, this way of defining, or redefining, problems in environmental toxicology could easily lead to superficial solutions the application of which could be hazardous. Biological systems have never been shown to be amenable to easy definition or representation.

Finally, one can hardly evaluate objectives that are not clearly stated. It is not easy for us to define well our objectives, especially for very exploratory studies. But the guidance clear objectives give us continues to make the effort important. And clearly stated objectives are absolutely essential if others are to be able to evaluate our methods.

B. EVALUATION OF METHODS IN ENVIRONMENTAL TOXICOLOGY

Even when objectives of biological research are clearly set forth, the evaluation of methods intended to make possible the achievement of these objectives is in no way a simple matter. In part, this is so because individual scientists differ in their views of the nature of biological systems and of what it would require to explain and so advance understanding of these systems. In consequence, except for the most limited objectives, biologists are apt to disagree as to whether or not particular methodological approaches are adequate. And because biological systems are complex, their adequate explanation is generally possible only through articulation of their different aspects, each of which may reasonably be approached methodologically in different ways. There is, then, considerable justification for a diversity of methodological approaches even to the same general objective.

In later sections, we will set forth our views of the nature of biological systems at conceptual framework and theoretical levels of understanding. For now, let us comment only briefly on three aspects of the evaluation of laboratory methodology: representational adequacy of the designed system, the adequacy of measurements, and the problem of interpretation. If we are to employ laboratory ecosystems, then representational adequacy, at the empirical level, pertains to whether or not the designed systems represent important aspects of natural ecosystems sufficiently well to make possible achievement of our objectives related to the natural systems. Studies of an intact living organism in the laboratory, however much we may modify its environment, are at least studies of a system that has acquired its design through evolution and development: the organism, itself, is a natural system and is representationally adequate for studies directed toward some important objectives. But it is another matter altogether where a biologist brings together in the laboratory groups of individuals of different species, maintains them under certain physical conditions, and begins to think of such an artifact as a laboratory ecosystem. Unless such a system is put together in light of considerable knowledge of some natural system it is intended to mimic, we have no reason to suppose that its measured behavior will be of any interest at all. Even when such knowledge is employed, the designed system is still likely to be dimensionally, relationally, and dynamically inadequate for attainment of objectives related to the natural system of interest.

Any laboratory ecosystem designed to be representationally adequate will have dynamic behavior that is determined by the number and kinds of species populations, their interrelationships, and environmental conditions. In its dynamic behavior, the values of its biological and physical variables may tend toward system steady states so long as environmental conditions are fixed. But even such a well designed laboratory ecosystem--of which we are aware of very few--has many potential steady states, which are determined by the levels of environmental variables. With changing environmental conditions, the system will not long persist in a given steady state. Measurements of system variables, then, can within broad limits be of almost any values, according to the state of the system when the measurements are made. These measurements represent time-variant behavior of the designed system, not simply variance to be dealt with statistically. If the system is not so well designed, measurements of its time-variant behavior may be of no interest whatsoever. Even good replicates of a well designed system are likely to be out of phase in their dynamic behavior, and the meaning of results determined only at one or a few times becomes difficult to ascertain.

This raises the whole question of how measurements on even very well designed laboratory ecosystems are to be interpreted. For we ought to know that had the measurements been made at a different time they in all probability would have been different. Moreover, were the levels of environmental factors to have been different, another pattern of dynamic behavior would then have occurred. And, of course, were one or more additional dimensions to have been included in the system there would probably have been completely different patterns of behavior. The interpretation of measurements requires that we have some *a priori* view that can give them meaning. Such a view may be held only subconsciously, but it must be there, as important philosophers of science have agreed.

We make measurements and we give them meaning: nature does neither of these for us. Moreover, when we design laboratory ecosystems, we in large part determine the capacities of these systems, their possible behaviors, and thus what measurements are possible. All this raises exceedingly difficult questions as to how we are to give meaning to the results of laboratory research on biological systems above the individual level of organization. Empirical generalizations, based on observational experience, give meaning only to the experience upon which they were based. We can know little about their generality--little about the boundary conditions of their application to nature.

Theory is another methodological approach science employs to give meaning to observational experience. From adequate theory, we should be able to deduce, and so explain, sets of important empirical generalizations. This tells us much more about the generality and applicability of empirical results. Moreover, however adequate a theory, much of its meaning derives from higher level conceptual constructs: the systems of consciously or subconsciously held beliefs about the nature of natural systems. For it is not only observational experience that determines what theories we find acceptable. These higher level conceptual constructs we will term conceptual frameworks, and we will distinguish clearly between these and the formal scientific deductive systems we call theories. In a later section, we will present a conceptual framework for biological systems, because we believe this and other such frameworks have important roles to play in empirical as well as in theoretical investigations. We believe that they can do this best if they are made explicit.

C. EXPLANATION AND UNDERSTANDING IN ENVIRONMENTAL TOXICOLOGY

Environmental toxicology, as a domain of human concern and applied science, is not unified by any common view or well articulated body of scientific knowledge. The interest groups and scientific disciplines involved are very diverse. Its being an area of common concern at all derives mainly from acknowledgment that toxic materials are being introduced into our environment, that sometimes the reasons for this appear very good, but that there are known and unknown hazards associated. And the full complexity of the matter is hardly perceived. Various biological and physical sciences are involved, but there is no general theory of toxicology--even at physiological levels, to say nothing about ecological levels of organization. There is some pertinent physical theory, however adequate it may be, but in toxicology we must finally deal with biological systems. The apparent goal of environmental toxicology would seem to be evaluation of the behavior and effects of toxic materials in biological systems, so as to make possible appropriate use and control of such materials. But just what such evaluation would ultimately need to entail is not at all clear. Mainly the effort until now has been empirical, and has proceeded through an increasing array of techniques providing results that are sometimes difficult to articulate and apply with any certainty at all. We have little general explanation and understanding of the phenomena with which we must deal. And without this our successes in dealing with toxic materials are likely to continue to be too few and too partial.

We suppose the goal of science to be the continuous advance of human understanding. Science works toward this goal by creating different sorts of explanations that make comprehensible and logically unify as much human perceptual experience as possible. Any explanation, most generally, can be taken to be a translation of the unfamiliar to the familiar that satisfies the need for explanation. To be an explanation, a statement or set of statements must increase understanding. But familiarity and satisfaction are relative. A language, or a statement articulated in a language, that is familiar to one person may be foreign to another. And even a familiar statement that, as an explanation, satisfies some may not satisfy others. Understanding is not advanced by proffered explanations alone but rather by these in interaction with the conceptual context within which they are received. Some commonality of language and conceptual constitution are *a priori* requirements for explanation and the advance of understanding.

Now to some the foregoing may seem rather far from environmental toxicology and the design and evaluation of laboratory ecological system studies. But we think it is important in this endeavor, because it lies at the roots of the possibility of scientific understanding and thus must also be the basis of environmental toxicology. We are here primarily concerned with the meaning of laboratory results and the application of these in the resolution of environmental problems. And man, not nature, gives meaning to his observational experience. How he does this is what science is all about.

To the early logical positivists, most notably Rudolf Carnap, the meaning of an explanatory proposition was its "method of verification." This was generally taken to be a deductive argument leading to logical consequences that could be related to observational experience, which was thus explained. Internal consistency and predictive power became the dominant criteria of explanatory adequacy, little attention being directed to conceptual presuppositions and other aspects of "external" adequacy of explanation. Nagel (1961), Popper (1959), and other philosophers recognized that theoretical constructs used in explanations do not in any simple way emerge from observational experience--that they are instead products of the scientific imagination. But these philosophers persisted in emphasizing internal consistency and verification or falsification by means of observational experience as the principal if not only criteria of explanatory adequacy. Some philosophers of science, certainly Kant, but more recently Hanson (1958), have insisted that the meaning of explanations comes as much from their encompassing contexts of preconceptions, beliefs, and background of knowledge of the persons involved as from the internal consistency and observational correspondence criteria emphasized by the logical positivists. Indeed, the meanings we associate with particular observational experience, say laboratory results, and thus the uses of results we are comfortable in making are equally dependent on such encompassing conceptual contexts.

In dealing with these philosophical matters pertaining to the conduct of scientific investigations, Warren, Allen, and Haefner (MS) employed a notion of the "conceptual continuum" of the individual scientist, which is illustrated diagramatically in Figure 1. This representation suggests that there are different levels of explanation and understanding extending from observation statements through empirical generalizations, models, theories, and conceptual frameworks to our funds of accruing experience and beliefs about the living world. Implicit in this is our conviction that observational experience and explanation at any level of such a continuum are understood only within the context of the whole. Thus the meaning we associate with results obtained from laboratory models--or any meaning we would be able to associate with such results--depends very much on available and operative theories and conceptual frameworks, whether or not these are made explicit. But only by making theories, conceptual frameworks, and other conceptual constructs and presuppositions explicit can we be rational in our consideration of the meaning and use of empirical results in environmental toxicology. Thus, in succeeding sections, we will deal with conceptual considerations and theoretical considerations as well as empirical considerations of importance in the design, conduct, and evaluation of laboratory research. And we must keep in mind that the results of such research in environmental toxicology are intended to reduce problems of toxic materials in natural systems.

But before beginning to do this, there are two other considerations that may be helpful. We have already noted that internal consistency is an important explanatory criterion: our arguments ought not to be self-contradictory. But they must also be externally adequate, or they are

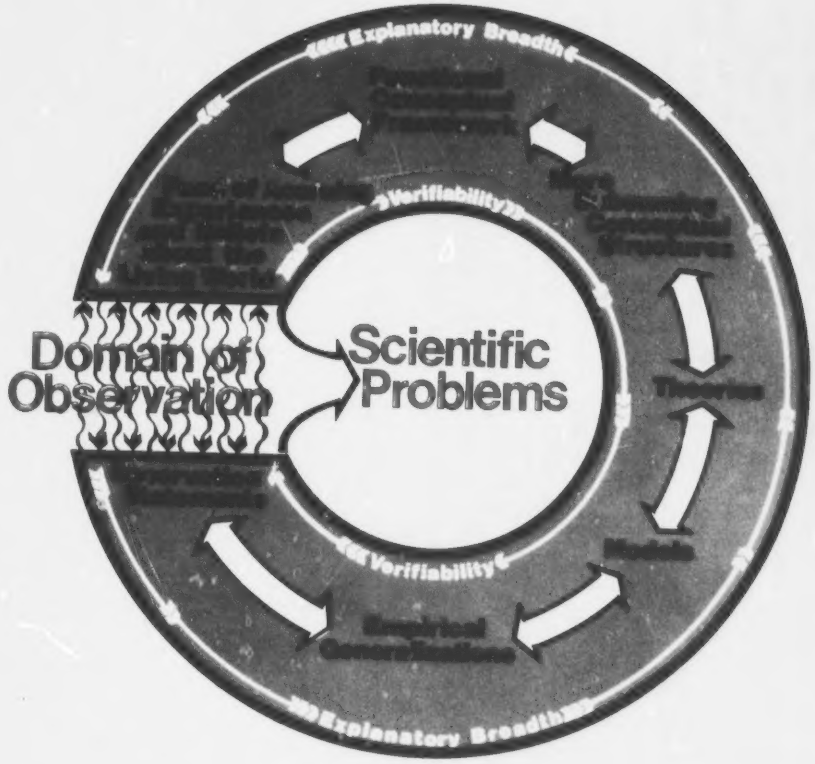
Explanatory Breadth
Verifiability
Domain of Observation
Scientific Problems
Conceptual Framework
Conceptual Structures
Theories
Models
Empirical Generalizations
Verifiability
Explanatory Breadth

Figure 1. The conceptual continuum of levels of explanation and understanding of an individual scientist. This is considered to be within the context of the scientific community. After Warren, Allen, and Haefner (MS).

irrelevant. Mere prediction is not enough: our explanations should account for what we know or believe to be involved in the natural systems we would explain. And because no explanation can be final, the heuristic power of explanations is another important criterion--their potentials for developing further more adequate explanations. Visualizability, another criterion, is involved in this. Aesthetic appeal may well be the ultimate criterion, because it would surely involve the other criteria, but it would also involve much more of our feelings about nature, which we ought not to dismiss lightly.

The final introductory consideration is the matter of universal explanation. Plato saw this as being possible only through abstract general and invariant forms, which were to be taken as being ultimately most real. This, of course, is idealism, which discounts the reality of the ever-changing and often apparently inconsistent flux of human perceptual experience. Physics, in the main, has followed Plato, with considerable success. Biology has more nearly followed Aristotle, the father of empiricism, who was suspicious of theoretical constructs and believed that universal explanation was implicit in the data of human experience. To many biologists, then, the answers to our questions-- the solutions to our problems-- seem to lie in the accumulation of more data. But this has not led to much if any universal explanation. We sometimes fail to remember that the data are the problem, for they must be explained, and this can be done only by conceptual constructs. More data do not usually decrease our difficulties of understanding, at least not directly so, because more data generally only show our previous understanding to have been incomplete; and even more logical unification of the whole then has to be done.

II. CONCEPTUAL CONSIDERATIONS IN ENVIRONMENTAL TOXICOLOGY

A. CONCEPTUAL FRAMEWORKS AS A PRIORI DESCRIPTIONS OF BIOLOGICAL SYSTEMS

Logical positivism, as a philosophy of science, largely ignored the context and origin of theoretical propositions and thus failed to account for scientific change. In his widely-read book, "The Structure of Scientific Revolution," Kuhn (1962) emphasized the priority of scientific "paradigms," within which normal science proceeds until serious difficulties are encountered. Solution of these problems sometimes requires new theories of drastically different form, and old rules may be broken to achieve these theories. Scientific revolutions occur with the crumbling and replacement of paradigms. Mainly as a historian of physics, Kuhn saw theories as setting the paradigms. And considering the great universality of the major physical theories, this may for physics be an adequate view. But Newton's dynamic laws and the general theory of relativity are no ordinary theories. For about 200 years, physicists could not even imagine a non-Newtonian world, and their work was governed accordingly.

In our opinion, biology does not yet possess this kind of universal theory. Thus we have no generally accepted *a priori* description of the biological world to guide our theoretical and empirical search for understanding. And, yet, biologists certainly have some conceptual basis for the judgments they continually must and do make in their theoretical and empirical investigations. But so long as that which they take to be *a priori* remains unarticulated in any readily accessible form, the rationality of their judgments and the adequacy of their theoretical and empirical work can hardly be evaluated. Gutting (1973) defined a conceptual framework as a description that subsumes theories and other conceptual structures pertaining to a natural domain, along with rules for employing such a description. To do so, such a description would need to be at a higher, more comprehensive, level of understanding, would need to be highly abstract, and would need to entail what most fundamentally and universally underlies all phenomena in the domain of interest. Warren, Allen, and Haefner (MS) tentatively proposed such a conceptual framework for biology, in which they articulated abstract concepts in a set of four natural language propositions.

The most enduring contribution of Immanuel Kant was his recognition of the logical necessity of *a priori principles and categories* for human perception and understanding. His principles were space and time--in which we perceive the form of objects--and causality, by which understanding of the interrelationships of objects is possible. Thus Alfred North Whitehead was to think of an event--an object or a system--as being four-dimensional in space and time. Now, whatever may be the nature of reality, the only world we could know must conform to the possibilities of human perception and understanding, as Kant so strongly emphasized. For us to perceive and understand a system, it must extend in space and time, and understanding may ultimately demand some notion of causality, even though the debates on indeterminacy will undoubtedly continue.

Thus, we will take a *biological system*, at whatever level of organization, to be composed of an *organismic system* together with its level-specific *environmental system* co-extending in space and time, as we attempt to illustrate in Figure 2. The biological system is not what we perceive in any momentary space-time section, but rather that which persists in space and time from some origin, through the present, to some future end. For any biological system, its present state can be understood adequately only in terms of its past and possible future states. This is why we think it logically most useful to define any biological system as the entire four-dimensional event, no matter how partially we may perceive it. Notions of causality will be evident in our statement and various interpretations of the following four biological system generalizations that Warren, Allen, and Haefner (MS) proposed.

1. *Any performance of any organismic system is an outcome of its operation, which consists of the interactive performances of its subsystems, and has functions or plays operational roles in maintenance, organization, or replication of the organismic system and a more encompassing system.*

2. *The potential capacity of any organismic system predetermines all possible sequences of realized capacities, which in turn determine all possible performances, any occurring sequence of realized capacities depending on the environmental system through time and any occurring performances depending upon the immediately effective environment.*

3. *Any performance of any organismic system requires space, time, energy, materials, and information, which are provided in particular forms and limited amounts by its co-extensive environmental system; potential and realized capacities determine the forms and amounts that will permit performance and thus determine the possible environmental systems within which the organismic system could persist.*

4. *Any organismic system tends to incorporate in some degree not only its organismic subsystems but also their particular environmental systems.*

We take this set of generalizations to provide a minimal *a priori* and outermost description of any biological system. To accomplish this, abstract theoretical, or primitive, terms are employed. Within limits set by their contexts in the generalizations, these terms can be interpreted in different ways so as to be applicable to explanation and understanding of biological systems on different levels of organization. Thus we will only interpret or illustrate such terms; we will not define them. This is a common practice in the development of theoretical scientific deductive systems, and it becomes even more important at the conceptual framework level of understanding (Fig. 1), if conceptual frameworks are to subsume entire domains of investigation.

The first generalization distinguishes between the *performance* of an organismic system as a whole, the *operation* of that system which involves the interactive performances of subsystems on successively lower levels of organization, and any *functions* or operational roles a performance of a

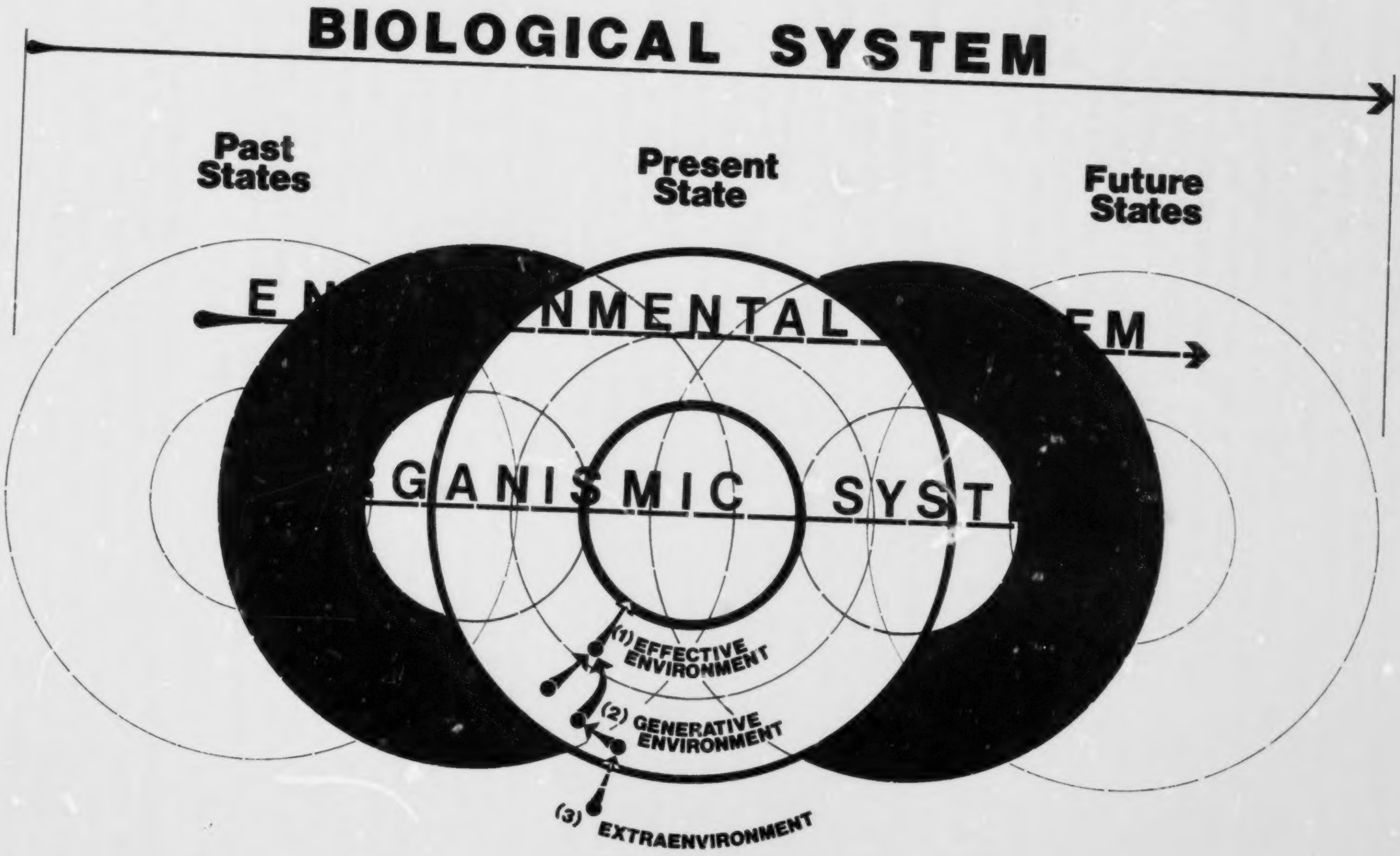
BIOLOGICAL SYSTEM
Past States
Present State
Future States
EN
NMENTAL
EM
GANISMIC
SYST
(1) EFFECTIVE ENVIRONMENT
(2) GENERATIVE ENVIRONMENT
(3) EXTRAENVIRONMENT

Figure 2. A biological system viewed throughout its existence as being composed of an organismic system together with its spatially and temporally co-extensive environmental system. After Warren, Allen, and Haefner (MS).

system may have in more encompassing systems. But the performance of any natural system is an extremely variant phenomena and cannot be universally--in a general and invariant way--explained in operational or functional terms. Thus, in Generalization 2, we introduce the notion of the *capacity* of an organismic system. Capacity is a very abstract notion of all possible performances of an organismic system in all possible environments. We cannot even conceive of a system exhibiting any performance for which it does not have the capacity. Nor can we determine, either theoretically or empirically, all possible performances of any organismic system in all possible environments. Yet any possible performance of any organismic system can be very abstractly accounted for as resulting from the capacity and the environment of the system. Thus a general, but very initial, explanation of performance becomes possible. We believe capacity to be the most fundamental notion required in biological explanation and that theoretical and empirical approaches ought to be evaluated on the basis of how well they deal with organismic system capacity.

Now it is generally recognized that the capacities of organismic systems change through time. Depending on the level of biological organization, this may result from either or both system development and system evolution. To deal with this, we must conceive of an organismic system as having some *potential capacity* that, through organization depending also on the prevailing environmental system, can lead to one of many possible sequences of *realized capacities*, as we attempt to illustrate in Figure 3. From the same initial potential capacity, the sequence of realized capacities will differ in different environments. And for a particular realized capacity, kinds and levels of performance will differ according to the then prevailing state of the environmental system (Fig. 3). We can think of organization, structure, and replication as being very general classes of performance, to be interpreted differently at different levels of organization.

Generalization 3 asserts the logically necessary relativity between an organismic system and its environmental system, which together form a biological system. This relativity has perhaps four aspects. First, an environmental system can be defined only in relation to a specified organismic system. Second, an organismic and an environmental system can only persist together; we can conceive of neither as persisting without the other. Third, in a very important sense, the potential capacity of an organismic system determines what sets of environmental conditions would be necessary for its persistence, and thereby predetermines all potential environments. And fourth, it is implicit in this generalization that the environment of an organismic system is specific to the level of organization of that system.

The important matter of the level-specificity of environmental systems can be made clear through illustration of Generalization 4, which asserts that organismic systems tend to incorporate the environments of their subsystems, as well as the subsystems themselves. Figure 4, among other matters, illustrates that other subsystems are in the environment of a particular subsystem, but, by definition, these cannot be in the environment of the organismic system as a whole. Beyond this, Figure 4 illustrates--for

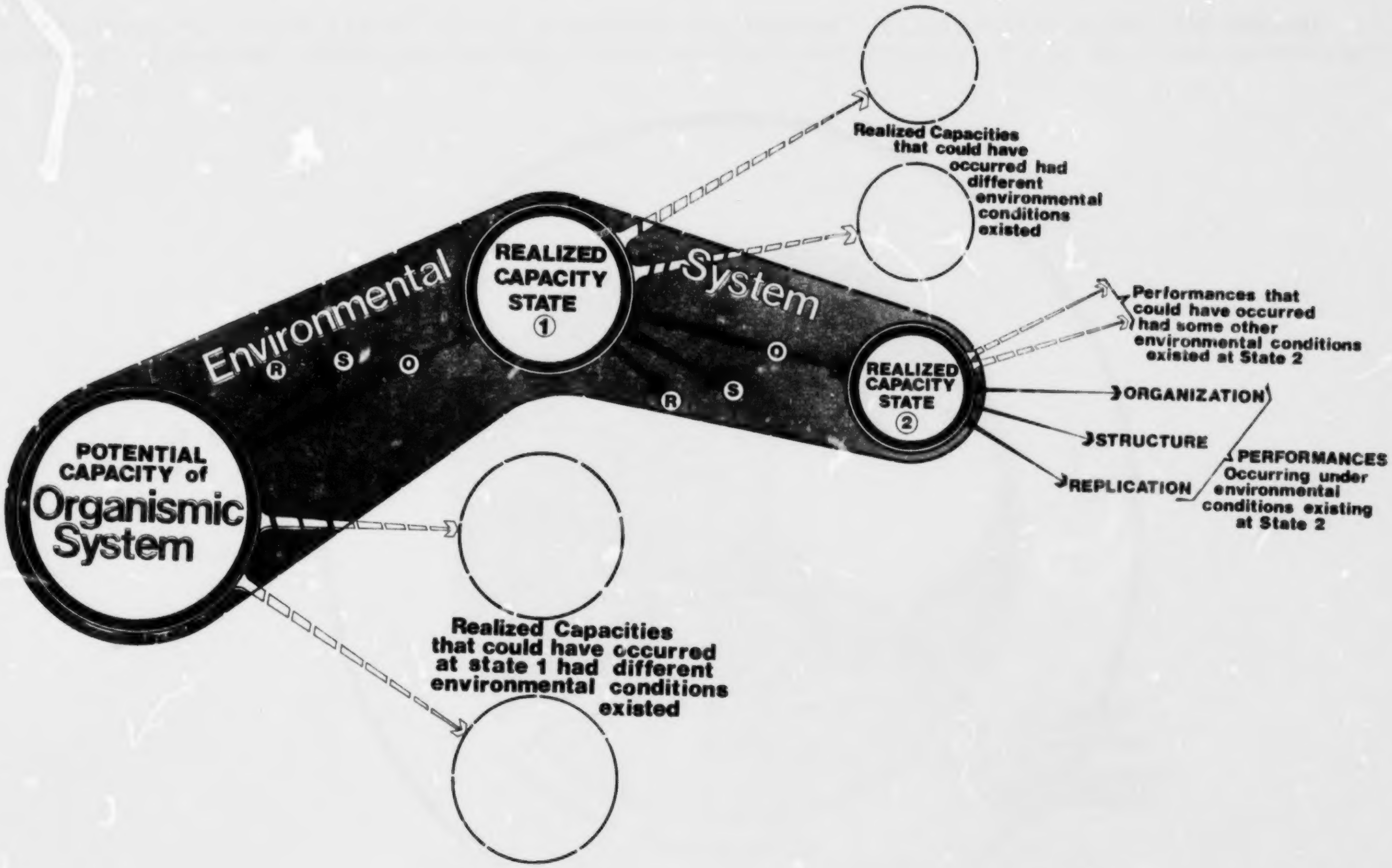
Environmental
System
R
S
O
R
S
O
POTENTIAL CAPACITY of Organismic System
REALIZED CAPACITY STATE ①
REALIZED CAPACITY STATE ②
Realized Capacities that could have occurred had different environmental conditions existed
Realized Capacities that could have occurred at state 1 had different environmental conditions existed
Performances that could have occurred had some other environmental conditions existed at State 2
ORGANIZATION
STRUCTURE
REPLICATION
PERFORMANCES Occurring under environmental conditions existing at State 2

Figure 3. A diagrammatic view of an organismic system showing that from some potential capacity the organismic system passes through a particular sequence of realized capacities jointly determined by its potential capacity and the actually prevailing environmental system. After Warren, Allen, and Haefner (MS).

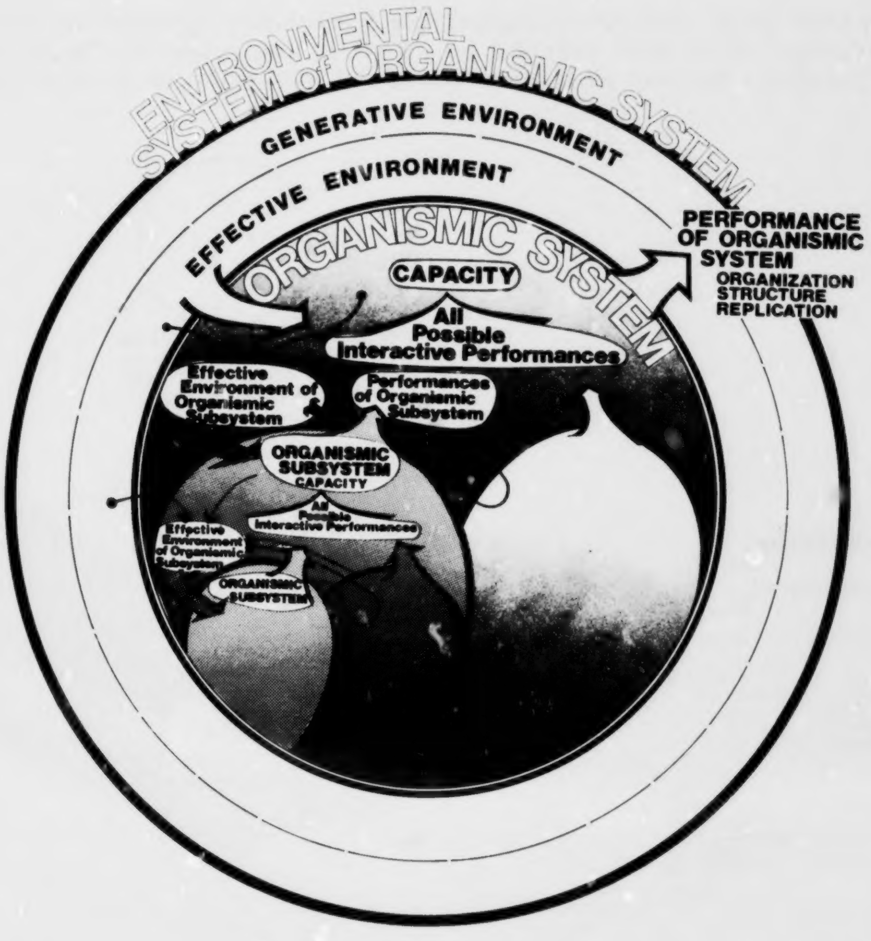
ENVIRONMENTAL SYSTEM of ORGANISMIC SYSTEM
GENERATIVE ENVIRONMENT
EFFECTIVE ENVIRONMENT
ORGANISMIC SYSTEM
CAPACITY
All Possible Interactive Performances
PERFORMANCE OF ORGANISMIC SYSTEM
ORGANIZATION
STRUCTURE
REPLICATION
Effective Environment of Organismic Subsystem
Performances of Organismic Subsystem
ORGANISMIC SUBSYSTEM
CAPACITY
All Possible Interactive Performances
Effective Environment of Organismic Subsystem
ORGANISMIC SUBSYSTEM

Figure 4. Organismic subsystems and their level-specific environments, all of which are incorporated by an organismic system having its own particular environment. After Warren, Allen, and Haefner (MS).

a single organizational state of an organismic system--the level-specific capacities of organismic subsystems as well as that of the system as a whole. The capacity of any subsystem on any organizational level determines all possible performances of that subsystem, actually occurring performances depending also on the state of its environmental system. Operation of the organismic system can be seen to be the interactive performances of subsystems on successively lower levels of organization, such operation leading to the performances of the organismic system as a whole. The functions of performances of the organismic system as a whole are to be seen in terms of the operational roles of these performances in some more encompassing organismic system.

Biological organization, from molecular to community levels, is characterized by ever more encompassing systems. The individual organism is one such level of organization, the biological population another, and the biological community an even more encompassing level. It must, however, be emphasized that there are important levels of biological organization between these commonly recognized ones. And especially we must emphasize that each organismic system on each level of organization has its own particular capacities and thus its own possible performances. Capacities and performances on different levels of biological organization are not the same. This has much to do with the design, conduct, and interpretation of laboratory studies in environmental toxicology. And we should also emphasize that only the performance of an organismic system can be more or less directly measured. Evaluation of the capacity and the operation of an organismic system--even though these are extremely important in explanation and application of results--must always be indirect and very partial.

B. ON THE NATURE OF BIOLOGICAL SYSTEMS

It must be apparent from the foregoing that we, at least, take the set of four generalizations presented earlier to define abstractly that which is essential to understanding of all biological systems. Our discussion and illustration of these generalizations and abstract concepts may have helped to make their intended meanings clear. But to be universally applicable throughout the biological domain, the generalizations themselves must remain abstract, so as to be variously and usefully interpretable as needed. Moreover, to deal with vastly different levels of biological organization, such a set of generalizations cannot say particular things in particular ways about particular systems. Still, to be of value in theoretical and empirical biological investigations, these generalizations must say what cannot be left out of our understanding of biological systems. They are intended to be employed in both heuristic and evaluative ways. But those of us who have been working with them, even though we have found them to be extremely useful in our own work, are under no illusions that they will be easily understood and readily accepted by others.

We must now proceed to interpret these generalizations for particular levels of biological organization that concern all of us working in environmental toxicology. In so doing, we will probably be able to make at least some of their possible meanings clearer, for to deal with particular levels of biological organization, it is not only legitimate but necessary to interpret abstract propositions in particular ways, thereby making them more visualizable. For now, we will interpret these generalizations only for the individual organism, the population, and the community levels of biological organization. In doing this, we will place particular emphasis on the differences in spacio-temporal extents, organizations, capacities, operations, performances, and functions of biological systems on these three different levels of organization.

Consistent with our view that adequate explanation and understanding of any organismic system in any state must be based on knowledge of previous states and possible future states (Fig. 2), we interpret an organismic system at the *individual organism* level of organization to be the entire possible *life history trajectory*. That is, the individual organism, as a system, is not simply what we may observe in space at any particular time but rather is the entire continuum of states from the zygote through reproductive maturity to death. Co-extensive in space and time with any developing individual organism is an *environmental system*, which changes as the needs of the individual organism change as well as with conditions influencing environmental factor levels. An individual organism together with its environmental system forms a *biological system* at the individual level of organization, which we take to be the *lowest level ecological system*.

The individual organism is composed of *physiological systems*: the organismic subsystems together with their level-specific environments, all incorporated in the individual organism and all having their own developmental trajectories. This brings us, then, to the matter of *organization* of the individual organism. We are free to interpret as is useful the diagramatic representation of an abstract organismic system shown in Figure 4. Many more than the two levels of organismic subsystems here shown are certainly present in individual organisms, and certainly there exists much greater complexity of subsystem interactions than that represented. What mainly we wish to emphasize is that an individual organism incorporates not only its organismic subsystems but their environments as well, that these organismic subsystems have their own capacities and performances, and that the performances are dependent both on capacities and environments. According to our theoretical or empirical investigational needs, we may differently interpret the levels of organization, but we should keep in mind that, with much overlap, there are in higher organisms certain *organ system*, *organ*, *tissue system*, *tissue*, *cell system*, *cell*, and still lower levels of organization. Even though the organization of some species, say man, at the individual level of organization has been much studied, not nearly all of the relations among such subsystems are known; neither, for that matter, have the subsystems been well defined. In defining subsystems and their interrelationships, we are approaching very near to causal or operational explanations, and these, of course, are always "written onto" the system for explanatory purposes, never observed. Few philosophers would disagree with this statement.

What are we to take to be the level-specific performances of an individual organism as a whole? Its *persistence* throughout its life history trajectory is perhaps the most inclusive performance of an individual organism. *Development* is necessary for this and is another very high level performance. *Structure* at any stage of development is also a performance of the individual as a whole, not only in that it is a result of development but also in that it is maintained operationally through the performances of lower level systems. And *growth* and *reproduction* are performances of individual organisms as wholes. *At most, we measure particular performances of whatever levels of organization.*

There are different ways in which we give meaning, explain, or come to understand such performances of individual organisms as wholes. *Operational* or complex lower-level causal explanations are one way. This is done by interrelating, as best we can, those relatively few measurements of performances of the subsystems of individual organisms we are able to make. This must always be done by conceptual structure, not observation, because we can never hope to measure all occurring performances of all subsystems, much less their interactions. *Functional explanation* is another way in which we give meaning to performances of an individual organism as a whole. This is done by defining a more encompassing organismic system, say a family or a population, of which the individual organism is a part. The functional explanation of a given performance, say reproduction, then becomes the operational role that the given performance plays in the organization and persistence of the encompassing system.

But we know that had the environment of an individual organism been different, most of its performances then would have been different. And we know that we cannot measure all possible performances of an individual organism in all possible environments. Still, we are aware that the persistence of an individual organism in nature depends entirely on its capacity to perform appropriately in a changing environment. Moreover, capacity itself changes from some original potential capacity--residing in the zygote--through some sequence of realized capacities, according to environment and throughout the life of the organism. In no way can such capacities be directly and fully evaluated. But the adequacy of biological explanation and understanding depends greatly on how well the capacity of individual organisms and other organismic systems is evaluated theoretically and empirically. Explanation and understanding in environmental toxicology are not exceptions to this.

We have now to interpret the biological system generalizations, and the figures illustrating them, at the population level of biological organization. This will necessarily be a more difficult interpretation than that for the individual organism level of organization. Whereas an individual organism is more or less directly observable--in other words, individual organism is an empirical concept--populations as wholes can in no ordinary sense be directly observed. Though it may sometimes be used as an empirical concept, the biological population concept is much more nearly a theoretical one. We will define a biological population, as an organismic system, to be a system of interbreeding organisms, more or less reproductively isolated from other such systems of the same species, from the origin of such a population to its extinction as a particular system.

Most populations are not simply aggregates of individual organisms but rather have their species-specific and even population-specific patterns of organization. Largely according to species, populations may have subsystems of *families, tribes, reproductive demes*, or other sorts of organization, and Figure 4 should be interpreted as necessary. Sex classes, age classes, size classes, and social classes are generally involved. What is important, here, is that the capacities and performances of any population are very much determined by the nature of its organization.

The performances of a population are specific to its level of organization, as are the performances of any defined organismic system. The *organization* of a population generally changes throughout its *"growth"* or *"development,"* which are to be taken as population performances. Organization of a population is also changed by *evolution*, a population level performance resulting from natural selection from among variant forms present in the population. The *structure*, or composition, of a population at any time is also a performance. And total tissue elaboration, or *production*, is a performance of populations. These and other population performances, together with the reproduction of its individual organisms, lead to the *persistence* of a population in space until its extinction. Persistence is thus very high-level population performance concept. Populations *replicate*, or "reproduce" themselves, but not in the same way as do individual organisms. We may think of a population as replicating itself when one (in the case of asexual reproduction) or more of its individual organisms leave the population and colonize a location sufficiently separated from the original for a distinct new population to arise.

For populations to exhibit such performances, which we can sometimes measure, they must have the capacities to do so (Fig. 3). To adequately explain population performances, as for performances of other kinds of organismic systems, we must evaluate population level capacities for growth, production, evolution, and persistence as fully as we are able. But, at the population level of organization, the evaluation of capacities becomes much more difficult than it is at the individual level. And yet, in a very real sense, it becomes more important to do so. For it is persistence of natural populations, not persistence of particular individual organisms, that most concerns man, except perhaps in his own case.

Operational explanations of population level performances are based on the interactive performances of individual organisms and other population subsystems. Functional explanations of population level performances are seen in the operational roles these play in more encompassing systems. These are of two sorts. The biological species as a system of populations, and the biological community, an altogether different sort of organismic system within which populations are involved.

We think it most useful to define a *biological community* not as a single, relatively short-lived, extant state but rather as the *entire series of states* from the origin of the community at some time in the past to some time in the future when it ceases to exist as a particular community. Over this rather long period of time, such a community develops from a "pioneer" seral community, through intermediate seral communities, to some sort of "climax" community, which is more persistent than the states or stages preceding it. This is the *community as the sere,* the entire developmental or successional sequence of seral and climax community states, which is another possible interpretation of the abstract representations of an organismic system given in Figures 2 and 3. We will think of such an object as an *organismic system* at the community level of organization. In no way do we wish to suggest that a biological community is any sort of an organism or superorganism. Rather, we view it and its co-extensive environment as a biological system definable by interpretation of the set of four biological system generalizations we advanced.

Two views of the nature of *plant communities* have dominated thinking of plant ecologists since early in this century. Unfortunately, these views have usually been taken to be mutually exclusive rather than to be representative of different aspects of the same natural systems. The *organismic view* of Frederic Clements (1916) and the *individualistic view* of Henry Gleason (1917, 1926) and L. G. Ramensky (1924) led to a largely fruitless controversy. Animal ecologists generally appear to have been either unaware of or disinterested in this controversy. Most of them seem to have accepted the existence of *biological communities* as concrete natural systems, which together with their physico-chemical habitats constitute *ecosystems*.

To Clements (1916) the community, metaphorically, was an organism "which arises, grows, matures, and dies....able to reproduce with essential fidelity the stages of its development." Here was the germ of one of the truly important theoretical concepts in all ecological thought. But many plant ecologists were distracted by Clements' logically improper use of analogy, his too direct application of this theoretical view to vast and sometimes fundamentally different organizations of extant vegetation, and his treating all differences in vegetation in physically different habitats as simply different manifestations of the same natural community to be dealt with by a burdensome system of classification. There ensued a failure to appreciate the best in Clements' thinking: a view of the community as a developing system necessary for adequate explanation.

To Gleason (1917), each plant community was fundamentally individualistic, not having the sort of genetic continuity that gives so much meaning to taxonomic classification of individual organisms, even though communities may be classified as a matter of convenience. He was more concerned with how individual organisms and species, according to their particular requirements, become involved in the development of what we take to be communities. Because each location on the earth is physically in some degree different from every other, because organisms of each kind are quite specific in their requirements, and because the opportunity for organisms to colonize different locations is not always the same, no two communities can develop in precisely the same way. Moreover, communities intergrade one with another, in such a way that their physical delimitation in space is generally difficult. Their definition as objects must be of a different sort than we employ in defining individual organisms. Gleason's view thus addressed an aspect of plant communities not accounted for in the view of Clements. Envisionment of the nature of natural systems that we might come to better understand them demands as full an account of their different aspects as we are capable of achieving at any given time. We must somehow make the best possible use of the insights of these two great plant ecologists, and all other relevant knowledge.

Failure to achieve a useful synthesis of these views of different aspects of communities resulted mainly from insistence by some that there be empirical demonstration of what communities are *in reality* and from failure to recognize that any explanation whatsoever presupposes at least some *a priori conditions* of understanding--ultimately the conditions of the possibility of knowing. Scientists implicitly or explicitly must make judgments related to the metaphysical problems of reality. But no philosopher or scientist has shown the way to solution of this problem since David Hume and Immanuel Kant raised the problem of metaphysics into high relief. Clements' view was of a plant community--the whole--as an object or system having four dimensions in space and time and capable of developmental performance and persistence. Gleason was more concerned with how such community level performances--development and persistence--resulted from the interactive performances of community subsystems, individual organisms and species populations, which are involved in the operation of the community as a whole and thus in its causal explanation. No view of community organization adequate for explanation can disregard either of these aspects, which lie at the very basis of the possibility of our knowing about communities. We must, then, direct our attention to what we may be willing to take as an *a priori*, outermost definition of what any biological community would have to be like for us to perceive and understand it, if we are to be able to develop a rational basis for the design and evaluation of laboratory ecosystem studies as an aid to understanding natural communities and problems of environmental toxicology.

As already noted, we take the four biological system generalizations we have advanced to be interpretable at the biological community level of organization. They thus constitute an *a priori theoretical view* of the fundamental nature of communities in relation to their environmental systems. But any such theoretical view of the nature of communities is of value only if it is reasonably interpretable in terms of what we take to be natural communities and their parts. Beyond this, it is the function of theoretical propositions to *order* observational experience so as to make it comprehensible, not merely to *reflect* observational experience as do empirical generalizations. Fundamentally, the problem of interpretation is the recognition of natural objects that could be expected to conform to the theoretical propositions. At any time, given what we take to be a community, what are we to take to be its subsystems? All too often, it seems to us, ecologists have tended to suppose that communities are simply the level of organization immediately above species populations, that communities can somehow be explained without taking into account intermediate levels of organization that may exist. But what might be these intermediate levels of organization, these subsystems lying between the community and its individual species populations?

This is not simply an empirical question, because how we choose to define such intermediate level subsystems will in large part determine observational experience and how we come to understand it. In any natural community, some populations interact more closely than do others. The individuals of some populations consume one another, compete for common resources, and may mutually favor one another. Such closely interacting populations can perhaps be usefully viewed as *trophic subsystems*, to be defined as a level above that of populations, in interpreting the abstract representation given in Figure 4. But surely some trophic subsystems interact more closely than do others, and this ought to be taken into account in any theoretical view adequate for community explanation. Trophic subsystems associated with trees and relationally involved plants and animals must interact more closely with one another than they do with the trophic subsystems associated with the shrubs, the herbs, or the substrate. Thus, we may be able to usefully think of a *tree subcommunity*, a *shrub subcommunity*, a *herb-grass subcommunity*, and a *substrate subcommunity*, together forming the community as a whole and each having its own trophic subsystems. In all this, there would necessarily be broad overlap of community subsystems at all levels, or we could not suppose the community as a whole to be a natural system.

Conceptualization and measurement of *performances* of organismic systems so extended in space and time and so diffuse in organization as are communities can be no simple matter. Community *persistence* is probably the most encompassing performance of an individual community. Community *development* or succession, through a series of successional communities or stages, is perhaps the most generally recognized community-level performance. And community *structure* at any time, just as change in structure with development, is a performance, and is the one that is most generally measured. Communities maintain individual organisms of many different species populations; and these sometimes leave the boundaries of a given community to become, through colonization, involved in the establishment of another community. This may perhaps be thought of as community *replication*. But such replication of a community is not precise, for the colonizers of communities may come from communities of different kinds. Communities have the *function* of maintaining the fauna and flora of a region, these being necessary to the establishment and persistence of the different communities in any region.

We reach a very high level of abstraction when we think of the *potential* and *realized capacities* of systems so abstract themselves as are biological communities. And yet, if communities have performances such as persistence, development, and structure, which they most certainly do--or we could not know of them--then it is logically necessary that communities have the capacities for these performances. In some sense, the capacities of communities are based on the flora and fauna of a region and on all possible interactive performances of the species of these.

C. ON THE ROLES OF CONCEPTUAL FRAMEWORKS IN ENVIRONMENTAL TOXICOLOGY

To many, if not most, of our readers interested in environmental toxicology, this lengthy and involved discussion of conceptual frameworks and the nature of biological systems may seem quite irrelevant to their work in toxicology. In all probability, our readers will not before have come upon a discussion quite like this, for we are unaware of any similar ones, even though we have searched. And, in all sincerity, we must confess that were we, for the first time, to have come upon such a burdensome presentation, we would be uncertain as to what it all meant--what role it might play in our thinking and work in environmental toxicology. But about 25 years of work in physiology, ecology, and environmental toxicology at our laboratory has convinced us of the need for explication of the conceptual frameworks within which we proceed in our theoretical and empirical investigations. Finding that others had not done so, and also that their work as well as ours exhibited weaknesses owing in large part to conceptual considerations, we were compelled to do what we could at the conceptual framework level of understanding, even in the knowledge that what we could do would be limited and surely require much continued effort on the part of ourselves as well as others. We now owe it to our readers to emphasize the necessity and roles we see for the sort of conceptual considerations with which we have been working.

In the introductory section of this report, we attempted to sketch the complexity of problems in environmental toxicology and of the social and natural systems within which these problems are perceived to occur. And there we emphasized that our theoretical and empirical investigations in environmental toxicology must relate in some way to these problems and natural systems, if there is to be much hope of resolving the rather serious toxicological problems we face. But how are we to evaluate our work, to identify and implement necessary improvements in our efforts to resolve these problems, and to recognize the limits or extent of applicability of our results to natural systems? In general we believe that adequately articulated conceptual frameworks have important *heuristic, evaluative,* and *application roles* to play in the conduct and employment of environmental toxicology.

To be effective in these roles, a conceptual framework must provide an adequate, *a priori*, outermost description of all biological systems, for only in so doing can it provide a conceptual context of theoretical and empirical work and its application. It must somehow be more universal--more general and invariant--than are the theories and results of empirical work it encompasses. This can be accomplished only with very high level theoretical propositions that in some abstract way include characteristics of biological systems that theories and empirical results either cannot or do not include. But the abstract concepts must be interpretable at particular levels of organization in particular ways, or they would be irrelevant to theoretical and empirical investigation and to what we take to be natural systems. The abstract biological system generalizations Warren, Allen, and Haefner (MS) tentatively proposed--in their considerable abstract universality and their various possible interpretations for different kinds and levels of biological systems--make possible much logical unification of our knowledge.

In providing a more comprehensive view of the nature of biological systems, a conceptual framework helps us to see more clearly the most important problems to be solved. Moreover, it helps to suggest theoretical forms and the designs of empirical investigations that are promising for our work in environmental toxicology. These are important heuristic roles.

A conceptual framework, insofar as it is adequate, should more nearly represent what is most important about biological systems and thus provide a basis for evaluating our theoretical and empirical work. At a minimum, because the framework is explicated, different pieces of scientific investigation can be rationally considered, even if there be disagreement about the validity of the *a priori* propositions. Such disagreement can rationally be resolved only by seeking out assumptions about nature even prior to these propositions. The rationality of science has suffered whenever there has been failure to do this. We believe that much theoretical and empirical work in biology can be evaluated in the light of the four biological system generalizations. Evaluation can be made more objective, within the conceptual boundaries of a framework, if its *rules* are made explicit. This is rarely done, even though rules of some sort are surely generally operative in science. Warren, Allen, and Haefner (MS) did derive from their conceptual framework at least some of the rules that seem to be implicit in it:

1. *Only the performance of an organismic system or subsystem can be measured, its capacity and its operation being representable only indirectly and incompletely.*

2. *Measurements of the performance of an organismic system or subsystem without relevant measurements on its co-extensive, level-specific environmental system are of little explanatory value.*

3. *Operational explanation of an organismic system should take into account the performances and operations of subsystems on successively lower levels of organization and cannot be based only on knowledge of subsystems on the lowest levels of organization.*

4. *Explanatory generalizations pertaining directly to any one level of organization of an organismic system should contain at least one concept specific to that level and should subsume conceptual, methodological, or other sorts of indeterminacy that may exist with respect to lower levels of organization.*

5. *Perception and explanation of organismic and environmental systems are always partial relative to the space and time dimensions and the components of the systems.*

Many biologists will find more acceptable the generalizations earlier reviewed than these rules we believe to be important, even though the rules appear to emerge quite directly from the generalizations. This is an inevitable consequence of making personal conceptual frameworks explicit. However this may prove to be, the rationality of judgments based on *a priori* generalizations and rules made explicit can at least be evaluated by others. The roots of any dissatisfaction with such rules should be sought in the generalizations from which the rules appear to us to follow quite directly. However others may feel about these particular generalizations and rules, we strongly believe that more effort of this sort is necessary in environmental toxicology.

There is at least one other kind of role articulated conceptual frameworks should be able to play in environmental toxicology: that is, as an aid in application of theoretical and empirical results to the solution of problems of toxic substances in our environment. In being at a higher conceptual level, such frameworks give meaning to theoretical and empirical explanations. Part of such meaning is in identification of boundary conditions, which must be taken into account in application of results to solution of problems occurring in natural systems. But there is also a positive aspect of further meaning we can give to theoretical and empirical work: it helps us to see ways of applying our results we might otherwise not have perceived. In later sections of this article, we will illustrate these heuristic, evaluative, and application roles of conceptual frameworks in theoretical and empirical investigation of environmental toxicology.

III. THEORETICAL CONSIDERATIONS IN ENVIRONMENTAL TOXICOLOGY

A. ON THE NATURE AND ROLES OF THEORIES AND MODELS

We have now to introduce theoretical considerations we believe to be of some importance in dealing with problems of toxic substances in man's environment. In doing so, we wish to distinguish clearly between what we have been calling conceptual frameworks and what we take theories to be. The generalizations of the conceptual framework do not themselves constitute a theory, and they are not intended to, because we envision them as operating at a higher level of explanation and understanding (Fig. 1). Theories, to accomplish their purpose, must make it possible for us to say more particular things about more precisely defined systems. We must now make clear what we, at least, take to be the nature and roles of theories and models. For, unlike in physics, there is in biology no general agreement as to what a theory may be, the term theory and the term model often being employed vaguely and even interchangeably.

Although it is not at all clear to us that adequate biological theory can have the same form as physical theory, we will in general restrict our meaning of theory to that employed in physics. Here, a theory is a *scientific deductive system* beginning with a set of initial propositions, at least one of which is a *theoretical proposition* by virtue of its involving a theoretical concept (Braithwaite, 1953). From the initial propositions, *theorems* are deduced by means of a calculus. But because the calculus itself adds no new meaning, any such theorems remain abstract, in that they still contain the undefined theoretical concept. For the theorems to be related to the perceptual world, *rules of correspondence* are employed to translate the theoretical concept into one or more empirical concepts--of phenomena more or less directly observable. Thus the theorems are translated into *empirical generalizations*, which are related only indirectly to the initial theoretical generalizations via the rules of correspondence and back through the abstract argument of the calculus.

In this way, empirical generalizations are explained by their deduction from theoretical generalizations. A number of different theorems may be deducible from the same set of theoretical propositions. These theorems, and any empirical generalizations into which they may legitimately be translated, are thus logically unified. Moreover, because the same theoretical concept can be translated, or interpreted, in different ways, a wider range of human perceptual experience can be explained. This is the *primary function* of any theory. But these very characteristics of theory, so understood, give it heuristic potential. Good theories are quite universal: they explain broad ranges of human perceptual experience in general and invariant ways.

This is something no empirical generalization can do. For all that can be deduced from and so explained by an empirical generalization are the same, or very nearly the same, observational experiences from which it was originally induced. Thus, without theory, we can know little about the meaning and generality of an empirical generalization. And therefore, say in environmental toxicology, we are unable to know with any certainty at all how generally an empirical generalization can be applied in the solution of problems. We can, of course, extend our knowledge of its generality and applicability by further empirical investigation. But there are so many differences in natural systems and the conditions under which they exist--and thus in the performances we might possibly measure--that we cannot hope to deal adequately with problems in environmental toxicology by empirical means alone. Moreover, were we to accumulate large amounts of data in attempting to determine the generality of some particular empirical generalization, we would usually find it to be very limited, and perhaps many different empirical generalizations to be necessary to describe these data. The reasons for this--or the relationships among these empirical generalizations and fundamental characteristics of any natural system of interest--would be unlikely to be obvious. But were we to be able to conceive of a set of theoretical propositions and a deductive argument making the empirical generalizations logical consequences, then we would have more adequately explained as well as logically unified not just the generalizations but the natural system itself.

There are very good reasons for distinguishing between *models* and *theories*. Models are made more particular and visualizable than theories, usually by empirical concepts, by analogy to observable systems--thinking of atoms as little solar systems--or by construction of physical representations. Theories are difficult to think about because they are abstract, and models of theories are sometimes employed, since in their particularity and visualizability the models help to alleviate this difficulty. But in so doing, models lose much of the universality of theories. Mathematical models are models rather than theories because their symbols are interpreted *a priori* in terms of observable events. Laboratory ecosystems are models of natural ecosystems, so long as our interest is in natural ecosystems, not simply in what happens in the systems we have created in the laboratory. They are models because they are representations composed of visualizable, measurable components. Such models make possible the generation of data that may be relevant to explanation of natural ecosystems. In this they share a characteristic with computer simulation models. Of course, the relevance of any such data to explanation of natural ecosystems depends very much on the representational adequacy of the model employed.

Judgments as to the representational adequacy of a model ought to take into account not only the objective the model was designed to accomplish but also all relevant theoretical and empirical knowledge of the natural system being modeled. If we are so fortunate as to have a formally articulated and rather universal theory of such a system, then the relationship between the theory and one sort of model is quite straightforward. By interpreting the abstract concepts in the initial propositions of the theory *a priori*--rather than *a posteriori* as is done with rules of correspondence in the theory--then the same calculus can be employed in both the model and the theory (Braithwaite, 1953). This mode of interpretation results in a more visualizable deductive explanatory system, as the model is, but it leads to loss of explanatory and heuristic power.

But even theories are partial in that they are apt to leave out something if not much of what we may know about natural systems of interest. Some of this other knowledge may be quite relevant to judgments about representational adequacy of laboratory ecosystems. It is for this reason that we placed so much emphasis on a conceptual framework and the apparent nature of biological systems. In any event, we must emphasize that models--whether they are of explanatory form or are employed only as "tools" of explanation--are almost always quite particular. What we can conclude from them is not likely to be very general: universal explanation and understanding require theories and conceptual frameworks.

With respect to theories, not all philosophers agree that they are explanations in any ordinary sense, that is, statements that might be characterized as true or false, good or poor. Some philosophers hold an "instrumentalist" view: theories are primarily logical instruments "for organizing our experience and for ordering experimental laws" (Nagel, 1961). Our own position, in what is really a continuum of beliefs as to the cognitive status of theories, is that they serve both functions remarkably well: universal theories are not only profound explanations, they are also powerful tools for explanation. Models that in some way translate what was unfamiliar into what is familiar and satisfy the need for explanation are also explanations. But, as we have already noted, models are more particular explanations; they do not have the universality of theories, even of the theories they may interpret. And models having some forms are not explanations at all. Laboratory ecosystems are not explanations, because data generated with such systems still need to be explained theoretically or otherwise. Laboratory ecosystems and other models sharing this characteristic are tools of explanation, ways of finding explanation, and they should be used in conjunction with theories and other explanatory systems whenever possible.

As to the form, function, and efficacy of models, we have noted two very different functions of models: an explanatory function and an instrumental or "tool-like" function. The form of a model very much determines whether it can be efficacious as an explanation, as a tool for explanation, as both, or as neither. Not only the evaluation but also the design of models ought to be based on their intended functions or objectives, for a model of a given form is not apt to serve several functions well, if at all.

Now models have many uses, some as explanations, some as aids to explanation, and some in making more apparent those phenomena that require explanation. Because models make the abstract notions of theories and other conceptual structures more concrete, visualizable, and manipulatable, they may serve as aids in the analysis of conceptual structures and the phenomena these represent. It is sometimes claimed that models are useful in further development of an extant theory. Braithwaite (1960), in a careful evaluation of the capacities of models, rejects some such claims but concurs that models may be of genuine assistance in theory development if they add hypotheses further relating the theoretical concepts of the theory or if they add hypotheses with new theoretical concepts interpreted in familiar ways. A model may suggest similarities in theories previously considered to be distinct and thus may show the way to bring two such theories together under a higher level theory; at least this is a claimed objective of modeling in general systems theory (von Bertalanffy, 1968). Beyond all this, models may be employed to outline problems and guide research effort, to generate new data, and to make predictions not always simply derivable from theories and other more abstract conceptual structures. Finally, we should not attribute to the theory characteristics of the model owing simply to its modality (Braithwaite, 1953; Nagel, 1961; Toulmin, 1960); yet, in our thinking about natural phenomena, we should never uncouple a model from the theory or higher level conceptual constructs it may only poorly represent.

Having considered the importance of keeping in mind the higher level conceptual structures from which models derive, let us return to the importance of designing and evaluating models according to their specifically intended functions, whether these be of an explanatory or of an instrumental nature. For carpentry, hammers are designed for pounding, screwdrivers for setting screws, saws for cutting boards, and planes for smoothing. A carpenter does not use a hammer for setting a screw nor a saw for smoothing a board. But neither does he use a ball-peen hammer for driving nails nor a large-toothed saw for finished cabinet work. And so it is with models, either as tools or as explanations. In the design and evaluation of laboratory ecological systems as models, our objectives--their intended functions--should be borne in mind, as should the conceptual structures by which we intend to give meaning to any derived results, or to relate these results to natural systems.

B. THE DYNAMICS OF ORGANISMIC SYSTEM PERFORMANCE

One of the functions of biological theories and models is to begin to explicate the effects of environmental factors on the performances of organismic systems. In this section, we will illustrate how a deductive argument developed by Booty and Warren (MS) can be used to examine some of the possible effects of changes in the levels of environmental factors on both dynamic and steady-state performances of simple multispecies systems.

In Figure 5A, a simple biological system is represented as a sequence of predator-prey interactions. The defined system is composed of interacting carnivore (C), herbivore (H) and plant (P) populations, and light resource level (R). Fishing effort (E) and rate of light input (I) constitute the environment of the defined system.

Phase planes and interrelated isocline systems representing this sequence of predator-prey interactions are shown in Figure 6. On each phase plane, prey biomass (or resource level) is plotted on the x-axis and predator biomass (or utilizer level) on the y-axis. The descending curves parameterized by light input rate (low I, med I, high I) on each phase plane are the prey or resource isoclines. Each prey isocline is a set of biomasses (or levels) of predator and prey at which the rate of change of prey biomass with time is zero ($dR/dt = 0$ on the PR phase plane, $dP/dt = 0$ on the H-P phase plane, and $dH/dt = 0$ on the C-H phase plane). The ascending curves on each phase plane are predator or utilizer isoclines. Each predator isocline is a set of biomasses (or levels) of predator and prey, at which the rate of change of predator biomass with time is zero ($dP/dt = 0$ on the P-R phase plane, $dH/dt = 0$ on the H-P phase plane, and $dC/dt = 0$ on the C-H phase plane). Each predator isocline is parameterized by a particular herbivore biomass on the P-R phase plane, by a particular carnivore biomass on the H-P phase plane, and by a particular level of fishing effort on the C-H phase plane. Each intersection of a predator and prey isocline, where the rate of change of both predator and prey biomass with time is zero, is a steady state point.

The forms, positions, and identities of all isoclines on the phase planes in Figure 6 have been graphically deduced from response functions that represent biological characteristics or performances of each of the interacting populations. Any population performance is determined by the population's capacity and its immediately effective environment, which includes other populations of predators, prey, and competitors. A deductive system, by logically unifying interactive population performances, can explicate performances of the higher level system of which the populations are parts. Such a higher level system, as a whole, is shown in Figure 5A. With the phase planes and isocline systems shown in Figure 6, the effects of changes in the level of environmental factors I and E on one of the performances of the defined system, its steady-state structure, can be determined. First, however, we will illustrate the graphical method of deducing predator and prey isoclines.

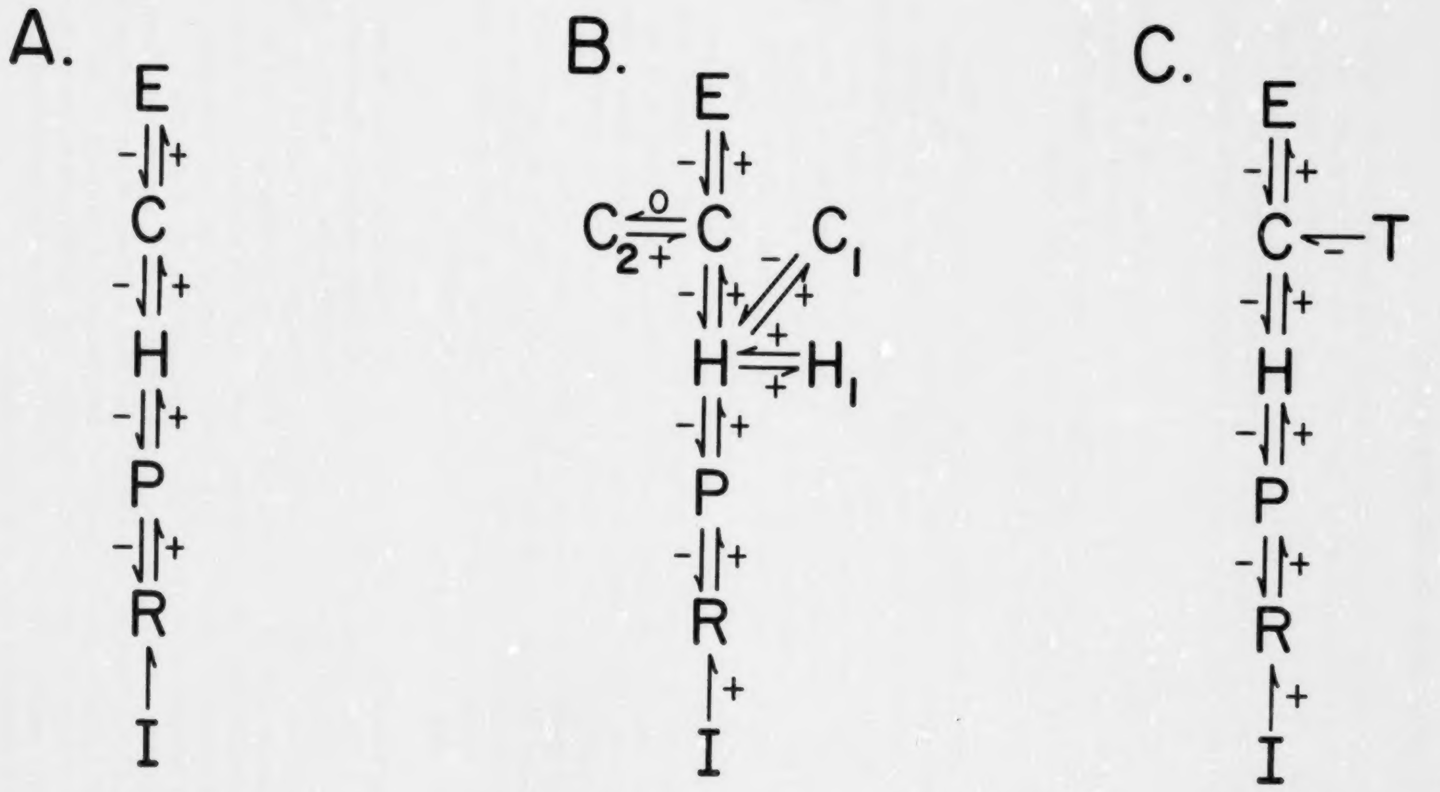

Figure 5. Kinetic diagrams representing defined multispecies system, including plants (P), herbivores (H), and carnivores (C). Rate of light input (I) and rate of exploitation (E) represent external environmental variables. Light intensity (R) is a variable dependent on I and P. Competition, commensalism, and mutualism are represented in B. And a toxicant (T) directly affecting only carnivore C is represented in C.

The form and position of the isoclines on each phase plane can be deduced from systems of curves representing such population performances as recruitment, production, loss to predation, nonpredatory losses, and yield to exploitation. Although there is a considerable body of theoretical and empirical knowledge of the forms of such curves or response functions, *we cannot expect to determine them empirically under the conditions defining them. Rather they are theoretical relations allowing us to take into account much of what we do know or wish to hypothesize.* Booty and Warren (MS) provide a detailed description of the graphical derivation of predator and prey isoclines on all phase planes. Here, only derivation of the predator and prey isoclines on the C-H phase plane will be shown. The same general procedure is used to determine the forms and positions of the isoclines on the P-R and H-P phase planes.

The position and form of the prey isoclines on the C-H phase plane are derived from response functions that represent performances of the herbivore population, as we show in Figure 7. The rate of change of herbivore biomass with time (dH/dt) is dependent upon the rate that the herbivore population gains biomass and the rate that it loses biomass. The population of herbivores in this simple community gains biomass through recruitment and production and loses biomass through consumption by carnivores (predation losses) and nonpredatory losses such as those owing to emigration and disease.

Herbivore recruitment and production gain curves are derived from the prey isoclines on the H-P phase plane and curves relating herbivore relative recruitment rate and relative growth rate to plant biomass. Derivation of herbivore production gain curves is illustrated in Figure 8. The prey isoclines (dP/dt = 0) on the H-P phase plane define density-dependent relationships between herbivore and plant biomasses at different rates of light input. A herbivore production gain curve and a herbivore recruitment gain curve can be determined from each prey isocline. Each production and recruitment gain curve is, therefore, parameterized by a particular light input rate. Herbivore biomass is removed from the herbivore population through consumption of herbivores by carnivores (predation losses, Fig. 7E) and nonpredatory losses (Fig. 7F). The recruitment and production gain curves of the herbivore for each rate of light input are summed to generate a set of curves representing the total gain rates of the herbivore (Fig. 7D). Similarly, the nonpredatory loss curve is summed with each predation loss curve to generate a set of curves representing herbivore total loss rates (Fig. 7G).

The prey isoclines on the C-H phase plane are defined as the sets of biomasses of carnivore and herbivore at which dH/dt = 0. When dH/dt = 0, the total rate of gain of herbivore biomass is equal to the total rate of loss of herbivore biomass. If curves representing total gain rates (Fig. 7D) and curves representing total loss rates (Fig. 7G) are plotted on the same graph, as shown in Figure 7A, the intersections of a gain curve identified by a particular rate of light input with a series of loss curves identified by carnivore biomasses define a set of biomasses of carnivore

Figure 6. Phase planes and interrelated isocline systems representing a sequence of predator-prey interactions in a simple community are shown in A, B, and C. The form and position of predator and prey isoclines on all phase planes have been deduced, with a graphical calculus, from response functions that represent the biological characteristics of each of the populations. An infinite family of prey isoclines exists on each phase plane. Each prey isocline is generated and so parameterized by a particular rate of light input I. The prey isoclines generated by three rates of light input, low I, med I, and high I, are shown on each phase plane. An infinite family of predator isoclines also exist on each phase plane. Predator isoclines are generated and thus parameterized by particular herbivore biomasses on the P-R phase plane; by particular carnivore biomasses on the H-P phase plane; and by particular levels of fishing effort on the C-H phase plane. The solid circles on each phase plane are steady-state points defining the steady-state biomasses of C, H, P, and R at high I, OE. The solid squares define the steady-state biomasses of C, H, P, and R at med I, 90 E.

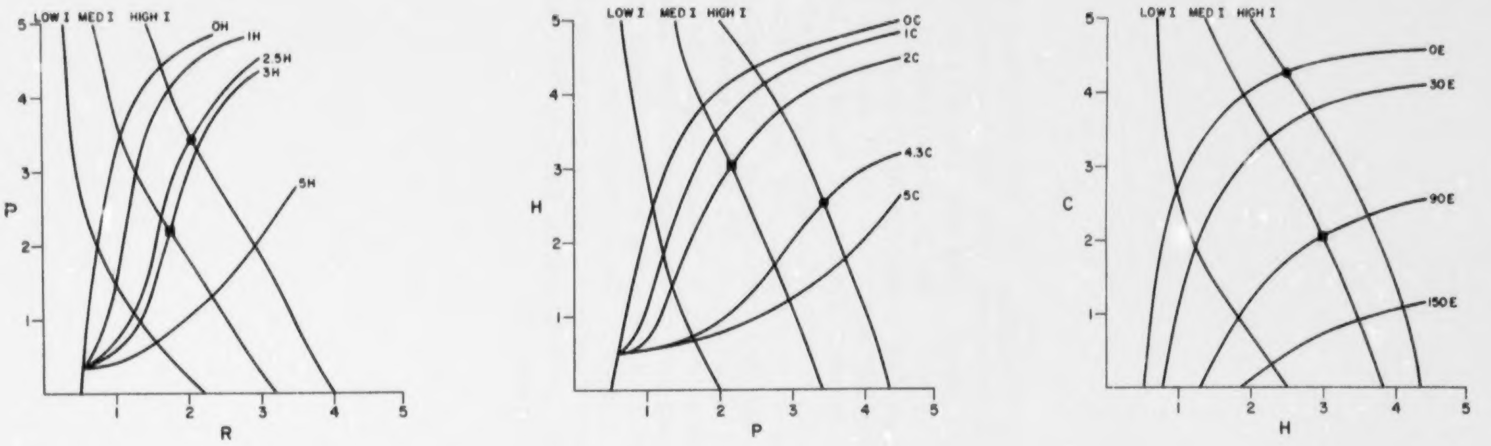
LOW I
MED I
HIGH I
0H
1H
2.5H
3H
5H
P
R
1
2
3
4
5
LOW I
MED I
HIGH I
0C
1C
2C
4.3C
5C
H
P
LOW I
MED I
HIGH I
0E
30E
90E
150E
C
H

Figure 6.

Figure 7. Derivation of prey isoclines on the C-H phase plane (Figure 6C) by graphical summation of herbivore gain and loss response functions. The prey isoclines on the C-H phase plane are the sets of biomasses of herbivore and carnivore where dH/dt = 0. The intersections of the curve representing herbivore total gain rates for a particular rate of light input I, with the series of curves representing herbivore total loss rates for different carnivore biomasses, C, (A) defines the set of herbivore and carnivore biomasses where dH/dt = 0. Each rate of light input generates and thus parameterizes a particular prey isocline. The curves representing the total gain rates of the herbivore (D) are constructed by graphical summation of herbivore recruitment (B) and production (C) rate curves for each rate of light input. The curves representing herbivore total loss rates (G) are constructed by graphical summation of the nonpredatory loss rate curve (solid line, F) with each predation loss rate curve (E). Total loss rates at 0C represent only nonpredatory losses. The nonpredatory loss rate response could also be represented by a family of curves parameterized by different levels of chemical, physical, or biological factors that would affect nonpredatory loss rate (dashed lines, F).

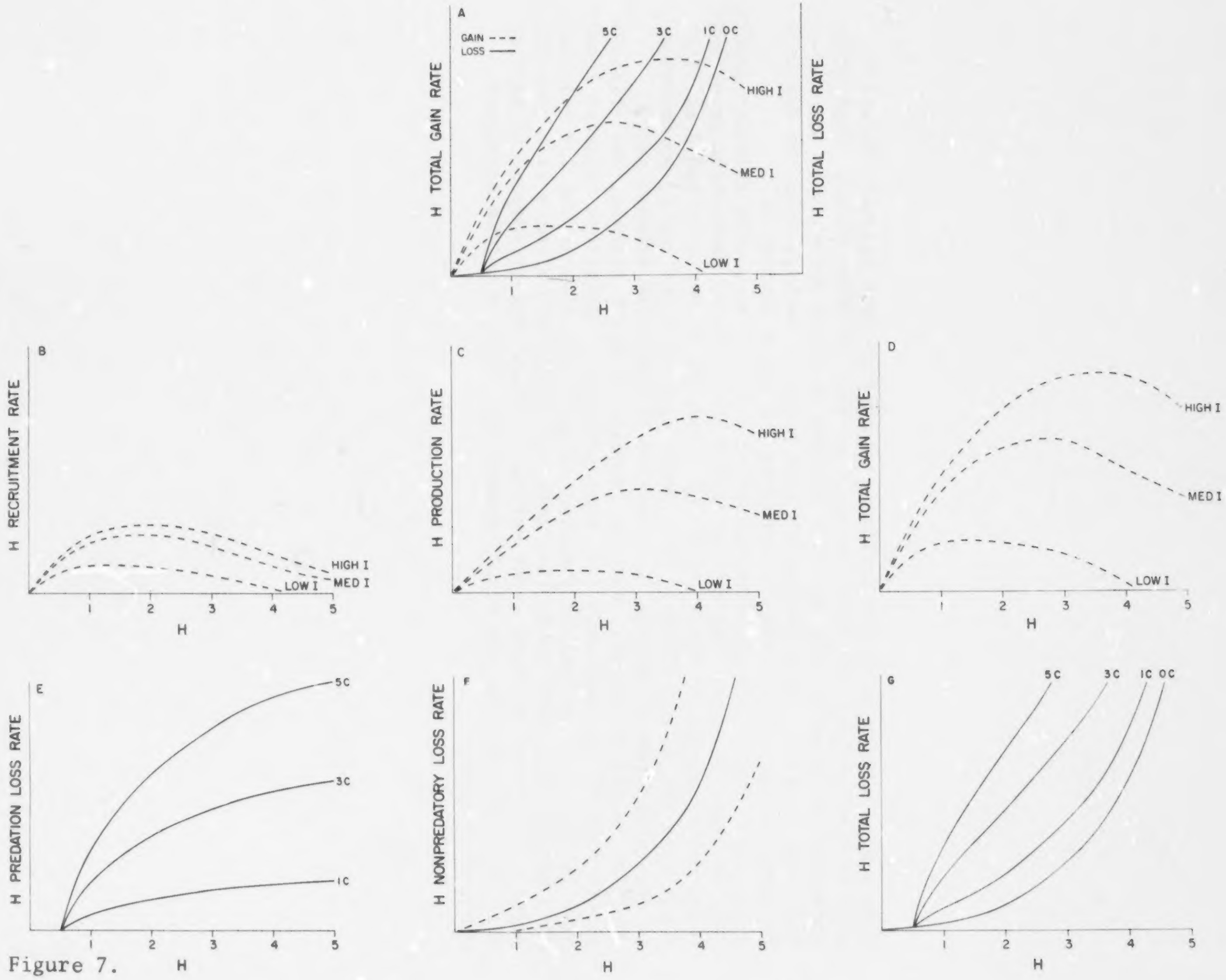
A
GAIN - - -
LOSS ——
H TOTAL GAIN RATE
H TOTAL LOSS RATE
5C
3C
1C
OC
HIGH I
MED I
LOW I
H
B
H RECRUITMENT RATE
HIGH I
MED I
LOW I
H
C
H PRODUCTION RATE
HIGH I
MED I
LOW I
H
D
H TOTAL GAIN RATE
HIGH I
MED I
LOW I
H
E
H PREDATION LOSS RATE
5C
3C
1C
H
F
H NONPREDATORY LOSS RATE
H
G
H TOTAL LOSS RATE
5C
3C
1C
OC
H
1
2
3
4
5

Figure 7.

Figure 8. Derivation of the herbivore production gain response functions used in constructing the prey isoclines on the C-H phase plane. Herbivore production rate is the product of herbivore relative growth rate and herbivore biomass. Each production gain curve is derived from the density-dependent relationship between herbivore and plant biomass at a given light input rate and from the curve relating herbivore relative growth rate to plant biomass. The determination of herbivore production rates from these relationships is illustrated for herbivore biomasses 1 and 3 at light input rate med I. In general, at a given rate of light input, an increase in carnivore biomass results in a decline in herbivore biomass and an increase in plant biomass. With an increase in plant biomass, the relative growth rate of the herbivore (gi) also increases. Herbivore relative growth rate is therefore an inverse function of herbivore biomass and the relationship between herbivore production rate and herbiv ore biomass is a dome-shaped curve. Each rate of light input defines a unique density-dependent reltionship between herbivore and plant biomass and, thus, a unique herbivore production curve.

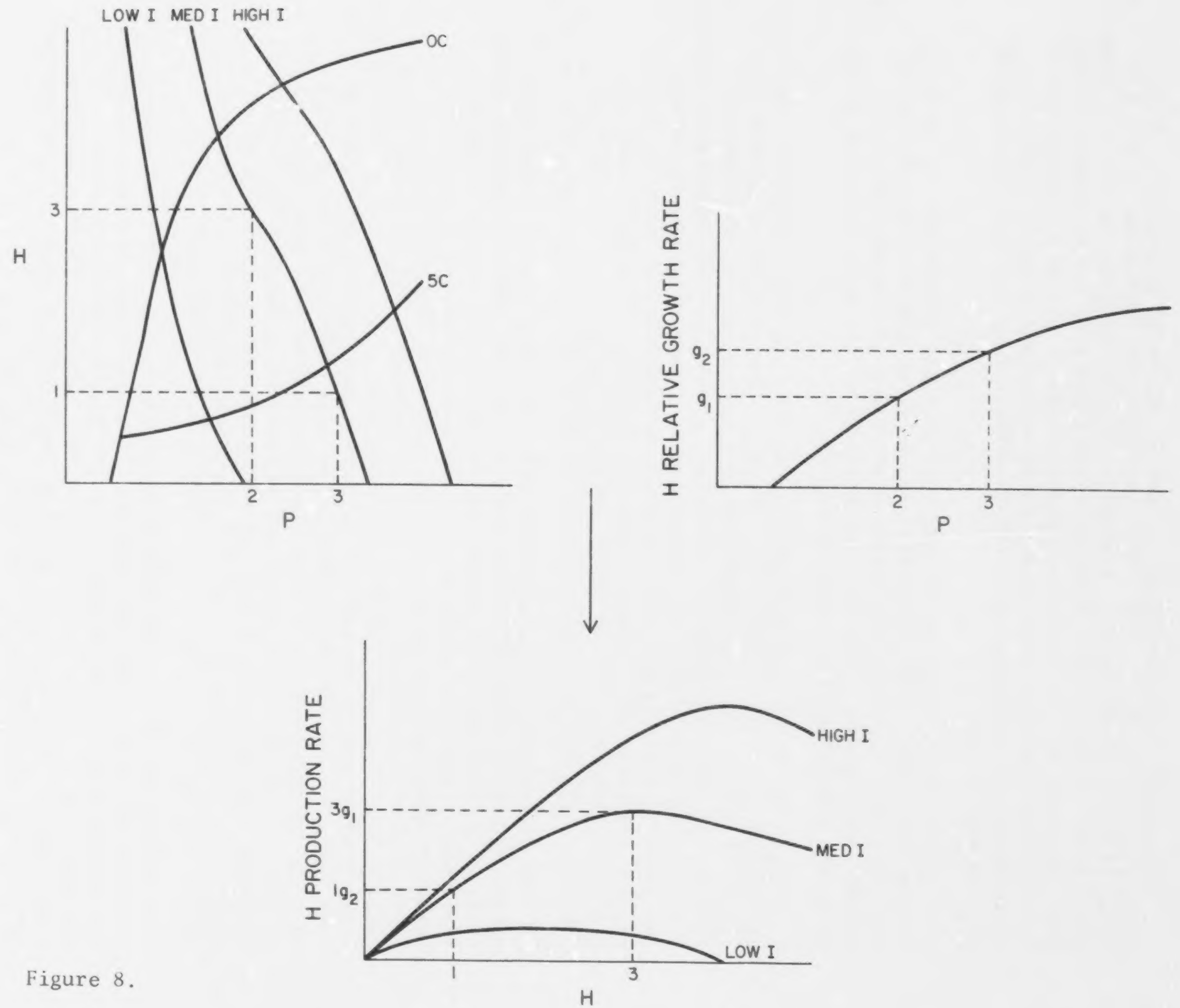
LOW I
MED I
HIGH I
OC
5C
H
3
1
2
3
P
H RELATIVE GROWTH RATE
g_2
g_1
2
3
P
H PRODUCTION RATE
$3g_1$
$1g_2$
HIGH I
MED I
LOW I
1
3
H

Figure 8.

and herbivore at which $dH/dt = 0$. That is, each rate of light input generates and so identifies a prey isocline on the C-H phase plane shown in Figure 6C.

In general, this procedure is used to derive prey isoclines on all phase planes. Rates of light input are initially introduced as the gain terms of R and so become the identities of prey isoclines on the P-R phase plane shown in Figure 6A. Rates of light input also become identities of prey isoclines on all successive phase planes. This is a consequence of constructing prey isoclines on any particular phase plane by utilizing recruitment and production gain curves derived from the prey isoclines of the previous plane.

Rate of light input is not the only possible parameterizing identity of prey isoclines. Any biological, physical, or chemical factor, including toxicants, affecting the response functions of a population would become an additional parameterizing identity of the prey isoclines derived from that population's response functions.

Essentially the same procedure is used to construct predator isoclines on the C-H phase plane (Fig. 6C): graphical summation of carnivore gain curves (recruitment, production) and loss curves (yield, nonpredatory losses), as shown in Figure 9. Carnivore production and recruitment response functions are solely derived, respectively, from a relationship between carnivore relative growth rate and herbivore biomass, as shown in Figure 10, and a relationship between carnivore relative recruitment rate and herbivore biomass. This method of determining carnivore gain response functions facilitates construction of predator isoclines.

Carnivore loss curves are represented by yield response functions, parameterized by level of fishing effort (Fig. 9E) and nonpredatory losses (Fig. 9F). Carnivore recruitment and production gain curves at each herbivore biomass are summed to generate a set of curves representing carnivore total gain rates (Fig. 9D). Similarly, the nonpredatory loss curve is summed with each yield curve to generate a set of curves representing total loss rates of the carnivore (Fig. 9G). The curves representing total rate of gain (Fig. 9D) and the curves representing total rate of loss (Fig. 9G) can now be plotted on the same graph, as shown in Figure 9A. The intersections of a loss curve (identified by a particular level of fishing effort) with a series of gain curves (identified by herbivore biomasses) define a set of herbivore and carnivore biomasses at which $dC/dt = 0$. Thus each level of fishing effort generates and therefore identifies a predator isocline on the C-H phase plane shown in 6C.

Having illustrated the deductive procedure used to determine the position and form of the isoclines on the phase planes in Figure 6, we can now examine the effects of changes in the levels of environmental factors I and E on the steady-state biomass performances of populations composing the defined system, and thus possible steady-state structures of the defined system shown in Figure 5A.

We can begin, on the C-H phase plane in Figure 6C, with the steady-state point at the intersection of the prey isocline parameterized by high I and the predator isocline parameterized by 0E. Progressively higher levels of fishing effort (0E to 150E) at this light input rate lead to lower steady-state C biomasses and higher steady-state H biomasses. In effect, then, increasing fishing effort moves steady-state biomasses downward on the prey isocline identified by high I, this reducing steady-state C biomass and, thus, allowing the steady-state biomass of H, the prey, to increase. Now, on the H-P phase plane at high I (Fig. 6B), an increase in steady-state H biomass leads to a reduction in the steady-state biomass of P, the steady-state values shifting up along the high I prey isocline with declining C biomass. And, finally, in Figure 6A, the reduction in steady-state P biomass resulting from increased H biomass leads to an increase in R.

Similarly, at a given level of fishing effort such as 90E (Fig. 6C), progressively higher rates of light input (low I to high I) lead to higher steady-state biomasses of both C and H, the location of the steady-state point now moving upward along the predator isocline identified by 90E. Increased I causes not only increases in C and H biomasses but also increases in P and R. Thus, changes in either I or E result, either directly or indirectly, in changes in the steady-state biomasses of all populations in this simple community.

There exists, then, for a given rate of light input and level of fishing effort, a single steady state on each phase plane, the set of these defining mutual steady-state biomasses of C, H, P, and R. In Figure 6, the steady-state points on each phase plane that define the mutual steady-state biomasses of C, H, P, and R--the steady-state structure of the defined system--at high I, 0E (solid circles) and med I, 90E (solid squares) are shown. Each of the three steady-state points in a set (either circles or squares) generated by a particular rate of light input and level of fishing effort is simply a two-dimensional projection of a four-dimensional community steady-state point. At high I, 0E, the populations composing the defined system attain steady-state biomasses of 4.3C, 2.5H, 3.5P, and 2R. Similarly, at med I, 0E, the steady-state biomasses of these populations are 2C, 3H, 2.2P, and 1.7R. Because there are conceivably an infinite number of particular rates of light input and levels of fishing effort, an infinite number of community steady-state points and, thus, steady-state community structures exists, each generated by a particular combination of light input rate and level of fishing effort.

In the foregoing discussion, only predator-prey interactions in a defined system have been considered. Somewhat greater dimensionality can be introduced by including, in the defined system, not only predation but also competition and commensalistic and mutualistic interactions between populations, as shown in Figure 5B (Booty and Warren, MS; Liss and Warren, MS). Biomasses of competitor, commensal, or mutualist become identities of prey and predator isoclines in addition to light input rate and level of fishing effort and, thus, also determine steady-state population biomasses, population persistence, and community structure.

Figure 9. Derivation of predator isoclines on the C-H phase plane (Figure 6C) by graphical summation of carnivore gain and loss curves. The predator isoclines on the C-H phase plane are the sets of biomasses of carnivore and herbivore where $dC/dt = 0$. The intersections of the curve representing carnivore total loss rates for a particular level of fishing effort, E, with the series of curves representing carnivore total gain rates at different herbivore biomasses, H, (A) define the set of carnivore and herbivore biomasses where $dC/dt = 0$. Each level of fishing effort generates and so identifies a particular predator isocline. The curves representing the total gain rates of the carnivore (D) are constructed by graphical summation of carnivore recruitment (B) and production (C) rate curves for each herbivore biomass. The curves representing carnivore total loss rates (G) are constructed by graphical summation of the nonpredatory loss rate curve (F) with each yield rate curve (E). The problematical yield response curves are determined from $dY/dt = qEC$ where q, the catchability coefficient, was fixed at 0.2. Total loss rates at OE represent only nonpredatory losses.

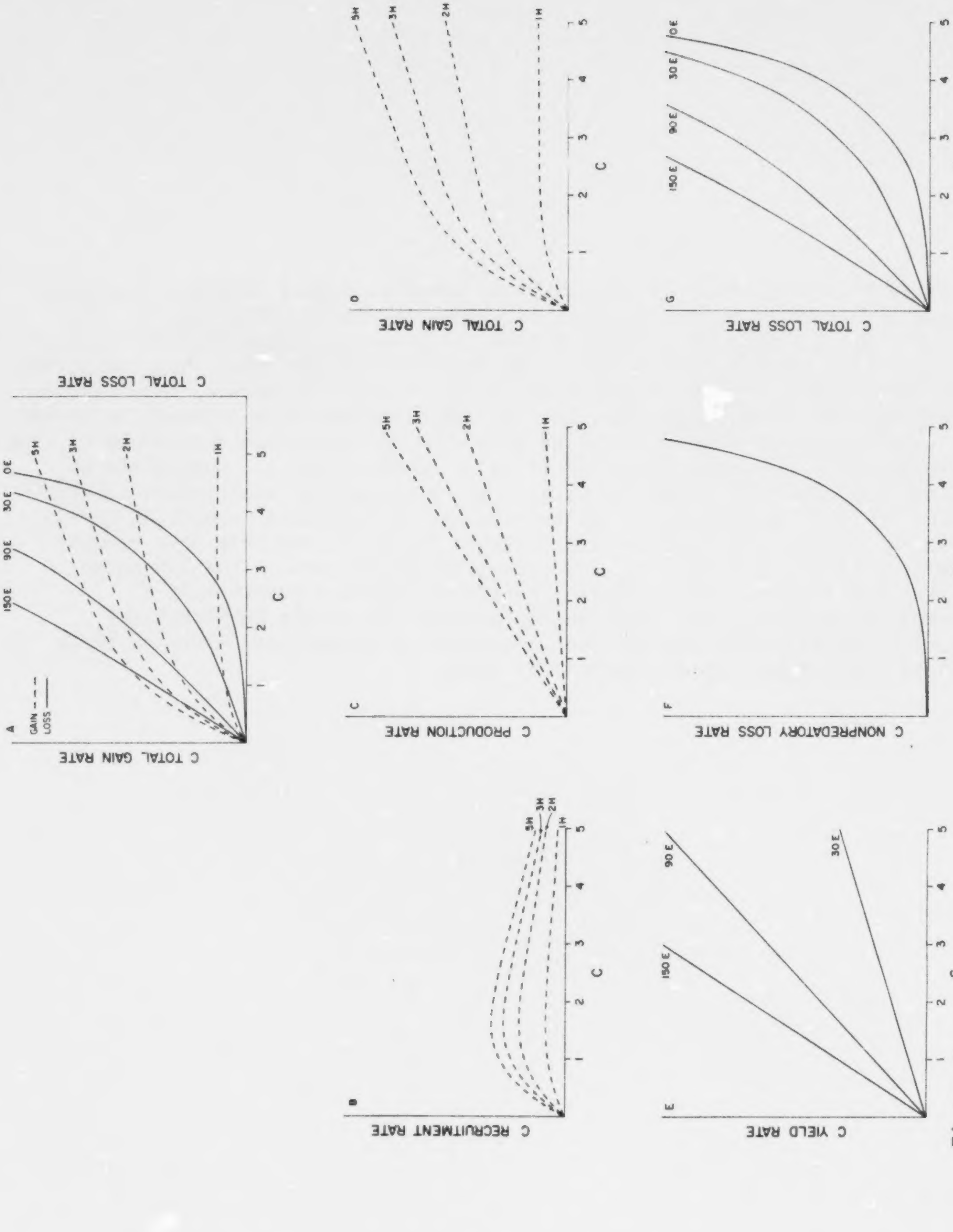
A
GAIN
LOSS
C TOTAL GAIN RATE
C TOTAL LOSS RATE
150E
90E
30E
0E
5H
3H
2H
1H
B
C RECRUITMENT RATE
C PRODUCTION RATE
D
C TOTAL GAIN RATE
E
C YIELD RATE
F
C NONPREDATORY LOSS RATE
G
C TOTAL LOSS RATE
C
1
2
3
4
5

Figure 9.

Figure 10. Derivation of the carnivore production gain response functions used in constructing the predator isoclines on the C-H phase plane. Carnivore production rate is derived from the curve relating carnivore relative growth rate to herbivore biomass. If herbivore biomass and, thus, carnivore relative growth rate were held constant at a series of levels, the relationship between carnivore production rate and carnivore biomass would be linear. Linear production responses can be generated for each herbivore biomass. The procedure is illustrated for herbivore biomasses 2 and 3. Derivation of these problematical carnivore production relationships facilitates construction of predator isoclines. System-determined carnivore production curves can be derived from relationships between carnivore and herbivore biomass defined by the prey isoclines at each light input rate on the C-H phase plane and from the curve relating carnivore relative growth rate to herbivore biomass. The relationship between the linear problematical production responses and the system-determined production curves at three light input rates (dashed curves) is shown.

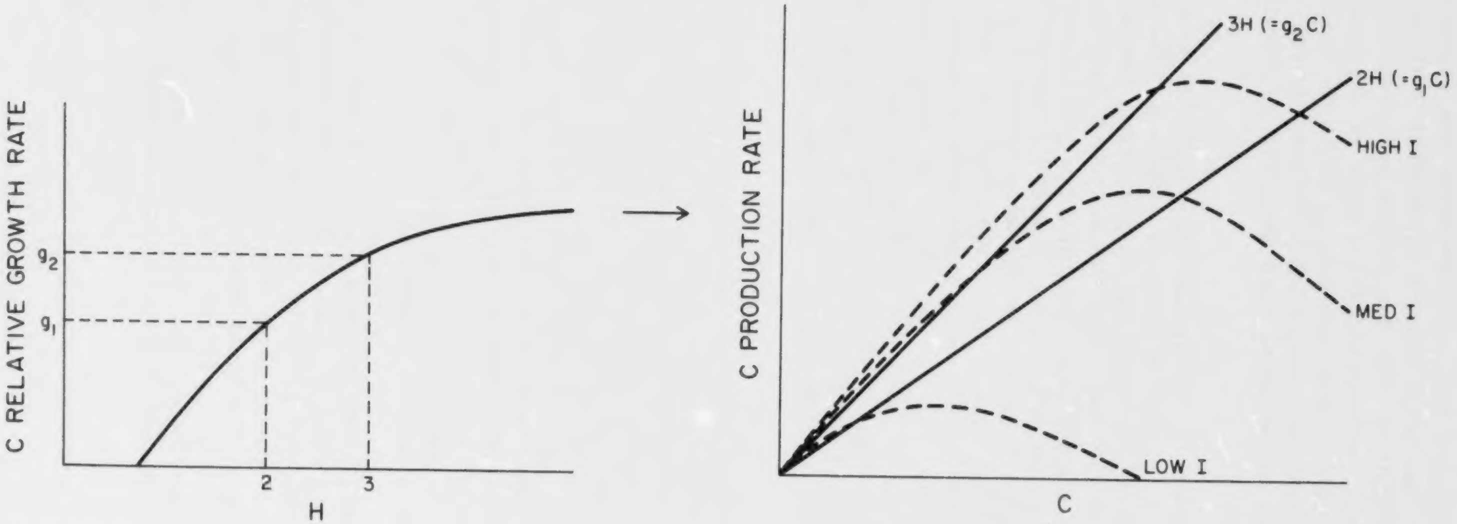
C RELATIVE GROWTH RATE
g_2
g_1
2
3
H
C PRODUCTION RATE
3H (= g_2C)
2H (= g_1C)
HIGH I
MED I
LOW I
C

Figure 10.

Environmental toxicologists seek to understand the effects of toxic substances on the capacity and performances of natural systems. Toxic substances introduced into natural systems induce perturbations in the performances of the systems: observationally, this is why such substances are first supposed to be toxic. Some possible effects of toxic substances on the performances of populations composing a defined system and on the structure of the system can be examined with the sort of deductive argument presented above.

The effect of a toxicant, T, *acting directly only on carnivore C* in the simple system defined in Figure 5C will be examined. To construct the isoclines on the phase planes representing this system, the effects of different concentrations of toxicant T on the response functions of the carnivore are defined. In Figure 11A, the relative growth rate response of the carnivore is shown to be reduced by increasing concentrations of T from 0T to 2T. The carnivore relative growth rate response is used to construct the carnivore production gain curves (Fig. 10) and, consequently, toxicant concentration in addition to herbivore biomass parameterizes the production response functions. In Figure 11B, a toxicant concentration of 2T is shown to be acutely toxic (toxicant induced mortality) to the carnivore. The remaining carnivore gain and loss response functions (recruitment, yield, and nonpredatory losses) are identical to those shown in Figure 9. In this example, toxicant induced mortality represents an additional loss response function.

In Figure 12, the phase planes and isocline systems representing the simple system defined in Figure 5C are shown. In addition to level of fishing effort, toxicant concentrations 0T, 1T, and 2T parameterize predator isoclines on the C-H phase plane. At a particular level of fishing effort, increasing toxicant concentration shifts the predator isoclines downward on the C-H phase plane, as shown in Figure 12. Toxicant concentration, as well as rate of light input and level of fishing effort, determine the steady-state biomasses of the populations composing the system and, thus, the steady-state structure of the defined system. The points locating the steady-state biomasses of C, H, P, and R at high I, 0E, 0T (solid circles), high I, 0E, 2T (solid squares) and low I, 90E, 2T (solid triangles) are indicated on the phase planes in Figure 12.

As yet, only the steady-state performances of a defined system at different levels of environmental variables have been considered. Environmental variables in natural systems may never be constant for long enough periods of time to permit these systems to reach steady-states. The dynamics of system performances and the response of the system to changes in levels of environmental factors, including toxicant concentration, are illustrated on the phase planes shown in Figure 12. Here, trajectories represent the changes through time in biomasses of populations composing the defined system.

If the levels of environmental factors I, E, and T are fixed at high I, 0E, 0T, from an initial point, O, simultaneous trajectories of biomasses on each phase plane (A trajectories) converge upon the points

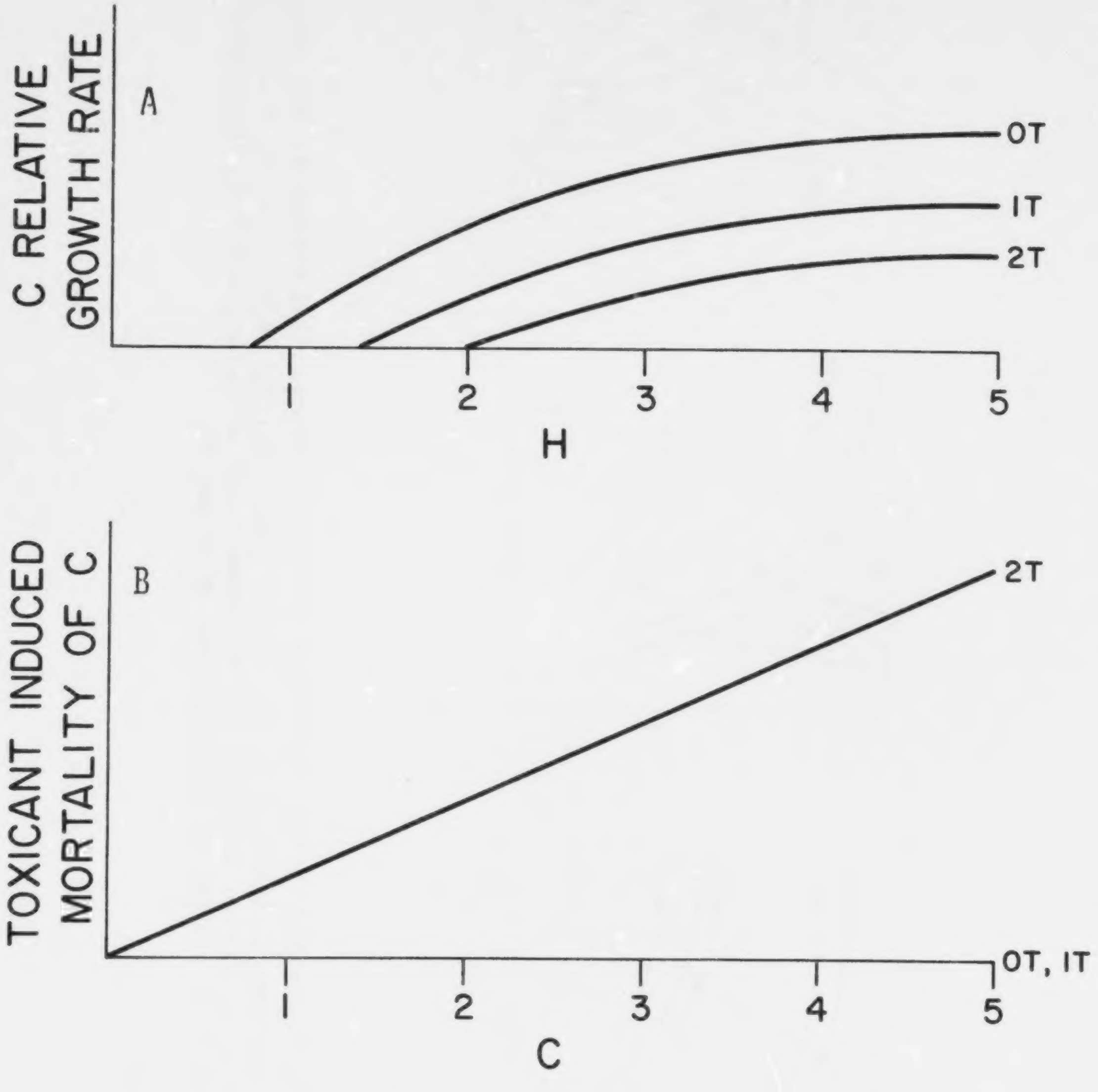

Figure 11. (A) Direct effects of toxicant T on the relative growth rate of carnivore C in relation to herbivore H biomasses, at concentrations of 0T, 1T, and 2T. (B) Direct effects of toxicant on the loss or mortality rate of carnivore C are shown to occur at 2T but not at 0T and 1T and are taken to be linearly proportional to biomass of C.

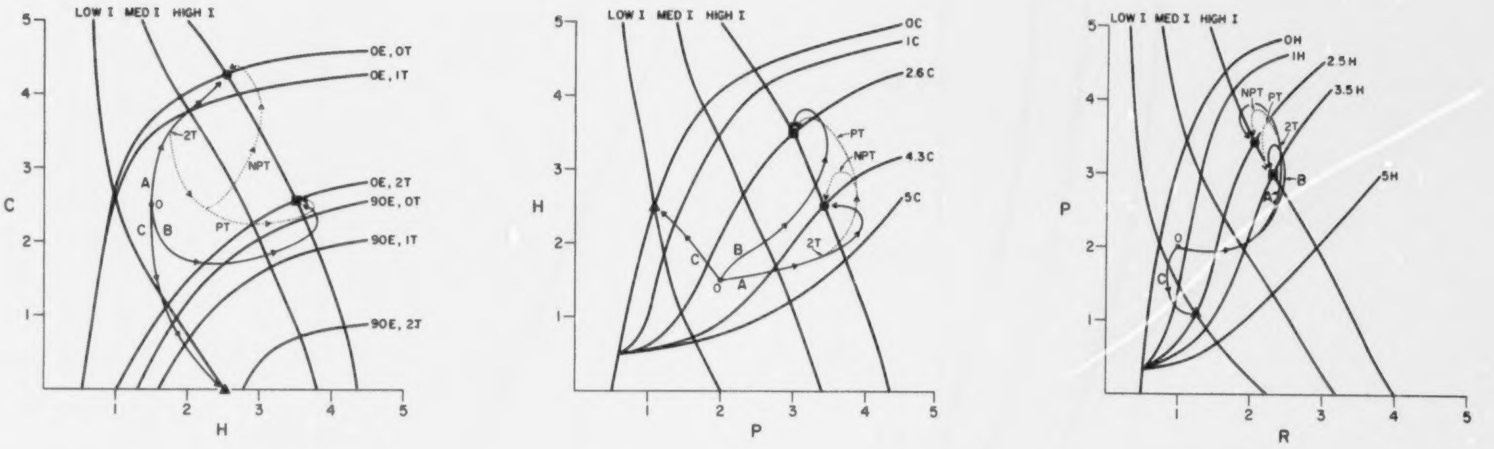

Figure 12. Possible steady-states (indicated by circles, squares, and triangles) and trajectories of biomasses of carnivore C, herbivore H, and plant P population and light intensity R under different rates of light input (low, medium, and high) and different level of fishing effort E, when toxicant T is absent and when it is present at concentrations of 1T and 2T.

locating the steady-state biomasses of C, H, P, and R (solid circles). On each phase plane, the steady-state point is a two-dimensional projection of a four-dimensional community steady-state point in hyperspace. Similarly, the A trajectory on each phase plane is also a two-dimensional projection of a four-dimensional trajectory that converges upon the community steady-state point.

If, after some period of time, a persistent toxicant (PT) directly affecting only carnivore C is introduced at a concentration of 2T, then the trajectories are perturbed and converge upon the points defining the steady-state biomasses of C, H, P, R at high I, 0E, 2T (solid squares). These are the same steady-state points upon which the trajectories converge if the toxicant is present initially at a concentration of 2T (B trajectories). If a nonpersistent toxicant (NPT) directly affecting only carnivore C is introduced at a concentration of 2T at the point so marked on the A trajectories, these trajectories are perturbed and progress toward the steady-state points generated by high I, 0E, 2T,initially by the paths of the trajectories resulting from introduction of the persistent toxicant. As the concentration of the nonpersistent toxicant in the system decreases, however, the trajectories begin to return to the steady-state points generated by high I, 0E, 0T on each phase plane. Through its effects on the carnivore population, toxicant T indirectly influences the performance of all populations and the structure of the defined system as a whole.

Now, if the levels of environmental factors I, E and T were fixed at low I, 90E, 2T, trajectories on each phase plane converge upon the steady-state biomasses of C, H, P, and R at low I, 90E, 2T (C trajectories). Under this set of environmental conditions, the prey isocline parameterized by low I and the predator isocline parameterized by 90E, 2T do not intersect on the C-H phase plane and the carnivore population is driven to extinction. Although carnivore C was capable of persisting at a toxicant concentration of 2T when I and E were fixed at high I, 0E (B trajectory on the C-H phase plane) the carnivore does not have the capacity to persist at 2T when I is reduced to low I and E increased to 90E (C trajectory on the C-H phase plane). Perhaps more than anything else, it is the capacity of systems to persist under toxic perturbation that we should seek to evaluate for biological systems.

The foregoing example serves to illustrate how the performances of systems are determined by the levels of environmental factors such as I, E, and the toxicant T. Changes in the level of any of these environmental factors alter the performance of the system. Ultimately, in environmental toxicology, we must attempt to understand how toxicants alter the domain of system performances. To do so, either theoretically or empirically, we must evaluate, insofar as possible, the performances of systems under different sets of environmental conditions. But we must always be aware that changes in species composition of a defined system, or evolution of these species, would change the magnitude and form of the population response functions and thus alter the positions and forms of isocline systems, the interactive performances of the populations, and the performance of the system as a whole. Thus increasing the dimensionality of the system to include a greater number of species and kinds of interactions (competition, commensalism, mutualism) would alter both time-variant and steady-state performances of the system.

C. THEORETICAL EVALUATION OF THE CAPACITIES OF ORGANISMIC SYSTEMS

Capacity is a theoretical concept that entails all possible performances of a system in all possible environments. Any organismic system has the capacity for an indefinite number of kinds and levels of performances, but the capacity of a system cannot be fully evaluated even theoretically. Theoretically and empirically however, partial evaluations of the capacity of systems to perform--their *scopes for performance*--can be achieved. Such a partial evaluation of capacity involves determination of particular performances of a system over a range of values of particular environmental factors. Theoretical evaluations of scope for performance should go beyond empirical evaluations of scope in explicating what the domain of performance of a system might be like and how toxicants might alter this domain.

An example of the use of theoretical determinations of scope for performance to give greater meaning to observational experience is found in the work of Taub (1973). Continuous flow culture of populations of the alga *Chlamydomonas reinhardtii* in the presence as well as in the absence of populations of the protozoan *Tetrahymena vorax* permitted Taub to determine, under different regimes of light intensity, flow rate, and nutrient concentration, some of the steady state population densities for the alga and the protozoa. With a simulation model, steady-state density isopleths for these two populations in relation to light intensity, flow rate, and nutrient concentration were derived (Fig. 13). Such systems of isopleths represent steady-state performances of the alga-protozoan system over a range of levels environmental factors and explicate the interactive effects of these factors in determining the scope for performance of the alga, the protozoan, and the alga-protozoan system. Introduction into this system of a toxicant affecting either or both the alga and the protozoan would have altered the scope for performance of the system and the domains of possible steady states under different environmental regimes.

D. ON DIMENSIONAL, DYNAMIC, AND EMPIRICAL ADEQUACY OF THEORIES

The logical positivistic emphasis of physics, as we earlier noted, has led to *internal consistency* and *prediction* as the primary criteria of theoretical adequacy. In mimicking the form of physical theory, biology has tended to adopt the same criteria. But evaluation of theory mainly on the basis of these two criteria leaves out too much of what we must expect of theories, if they are to be adequate for biological explanation and understanding. Before we go on to elaborate what further *external adequacy* we should expect of biological theory, however, let us consider briefly what may be meant by prediction, as it is certainly important. First, prediction as a test of the adequacy of theory is very powerful if, by prediction, we mean the identification of some previously unknown event,

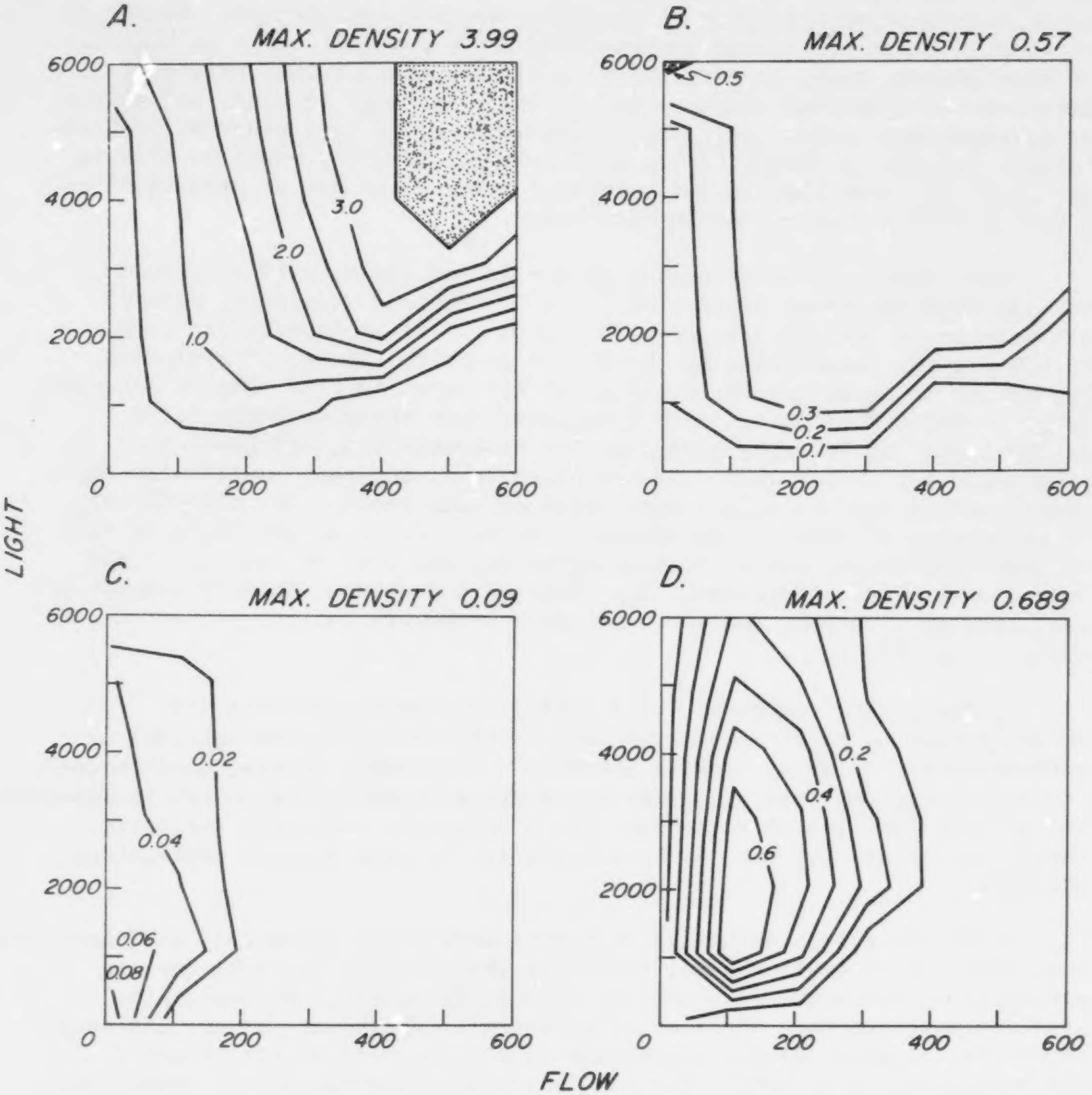

Figure 13. Steady-state density isopleths of the alga *Chlamydomonas reinhardtii* (A and B) and the protozoan *Tetrahymena vorax* (C and D), under different light and flow regimes when nitrate supply was 0.5 mM (A and C) and when it was 0.05 mM (B and D) in continuous flow cultures. These diagrams illustrate population scopes for performance in terms of steady-state biomasses and environmental variables. After Taub (1973).

say a new subatomic particle, that we then find a way of observing or detecting. To make this sort of prediction possible, it would appear that a theory somehow logically incorporates important aspects of the underlying nature of the natural system. But, at least in biology, it is not our impression that this is what is generally meant by prediction. Rather it is usually taken to be some statement about the probable value or behavior of some already known object. If a theory can predict such values or behaviors of a natural system under a very wide range of kinds and values of environmental conditions, prediction again would be a powerful test of theory, for only a theory having much external adequacy would be able to do this. But even this is not generally expected by way of prediction as a use or even a test of biological theory.

What, then, are we to expect in the way of adequacy of theories? We will consider three aspects of this: *dimensional adequacy*, *dynamic adequacy* and *empirical adequacy*. Lewontin (1974) employed these terms in his critical evaluation of the modern genetical theory of evolution, but we may be extending the meanings of his terms further than he intended. We do so because it is our deep conviction that theories ought to be explanations considerably advancing our understanding, and prediction alone does not insure this. On the other hand, adequate explanation and understanding tend to insure prediction of both kinds. In considering these aspects of theoretical adequacy, we must do so in the light of what we take explanation and understanding to be, and what we take to be the nature of biological systems. The external adequacy of theories cannot be evaluated in a vacuum, and the conceptual framework earlier presented can serve as an aid.

By *dimensional adequacy* of a biological theory, we mean its incorporation of sufficient organismic system variables and external or environmental variables to make possible a reasonably general explanation of the behavior of natural organismic systems to which the theory is directed. And we take "sufficient variables" to be naturally important variables, enough variables, but not too many variables to make general explanation possible.

In the graphical deductive arguments previously presented, we demonstrated that addition of environmental variables changed both the *behavior* and *steady-state structure* of a defined organismic system. We could also have demonstrated that addition of organismic dimensions--or objects--would change the *capacity* of the organismic system, as well as its behavior and structure. Even apart from any deductive argument, we all intuitively know the importance of addition or deletion of variables from a system defined to represent some natural system. But natural biological systems, say biological communities together with their physical environments, may have thousands of variables. Surely the relatively few dimensions with which we can deal adequately cannot represent such biological systems.

We believe adequate theoretical representation and explanation of dimensionally complex natural systems require definition of objects of these systems at a high enough level to reduce the number of dimensions needing representation. For the biological community, such objects may be community subsystems, which include trophic subsystems made up of populations. Only for systems lower than the community level should populations be represented as objects in a theory. The dimensions that we do include should make it possible for us to evaluate aspects of the capacity of a system, not simply its performance under a particular set of environmental conditions. But no theory of which we can conceive can fully evaluate the capacity of a natural system.

By *dynamic adequacy* of a theory, we mean reasonably general representation of the behavior--both time-variant and steady state--of the natural system toward which the theory is directed. A theory cannot be dynamically adequate if it is dimensionally inadequate. But dynamic adequacy involves the *adequacy of relations* among variables hypothesized in a theory, as well as the number and kinds of variables included. For relations, just as much as dimensions, will determine the behavior, structure, and capacity of the theoretically defined system, and thus how well this explains the natural system of interest.

Relational adequacy raises difficulties perhaps even greater than those raised by the dimensional adequacy criterion. This is because we may more or less directly be able to perceive the objects we identify as dimensions, but we can in no ordinary sense observe the relations between, or the interactions of, the performances of these objects. To suppose that we can is to ignore all the difficulties of causal explanation philosophers have been unable to solve. Thus we hypothesize relations among objects or their performances. The addition of many dimensions to a theory or simulation model only aggravates the difficulty of hypothesizing reasonably adequate relations among dimensions.

Now what do we mean by *empirical adequacy* of a theory? In a narrow sense, the theorems of a theory must be translatable into empirical generalizations, the conceptualized identities of which can be adequately observed. Otherwise, the theory is irrelevant. But, more generally, to be empirically adequate a theory must account for the performances we are able to measure, and do so under ranges of environmental conditions and system states of general interest. Again, this is only to say that a theory must to some useful degree permit us to evaluate the capacity of the organismic system of interest, this ultimately involving empirical as well as dimensional and dynamic adequacy. An empirically adequate theory must give meaning to particular performances we measure, and it must do so by relating these performances to other performances on the same level of organization as well as on lower and higher levels of organization. It must do so in a way making it possible for us to know at least theoretically, the *possible applications* of empirical results we obtain in the laboratory or in nature.

IV. EMPIRICAL CONSIDERATIONS IN ENVIRONMENTAL TOXICOLOGY

A. ON PROBLEMS OF CREATING BIOLOGICAL SYSTEMS IN THE LABORATORY

Good empirical investigation is important in any science, for empirical results are our perceptual interface with nature. Good empirical generalizations reflect something of nature, even if they fail to order nature as do universal theories. This makes it important that laboratory research in biology be conducted so as to yield the most general results possible. Moreover, such research helps to make clear what there is about nature that we must develop conceptual frameworks and theories to explain and understand. We must, however, employ extant conceptual frameworks and theories, inadequate though they may be, in the design, evaluation, and application of empirical research. In this part of our consideration of laboratory research in environmental toxicology, we will deal with problems of creating biological systems in the laboratory. Then, in following parts, we will consider determination of organismic system performances and evaluation of capacities as well as the adequacy of empirical investigations in environmental toxicology.

Before beginning, perhaps we should note again our definition of a *biological system:* an *organismic system,* whatever its level of organization, together with its level-specific and *co-extensive environment,* extending through all states of the organismic system from its origin to its end (Fig. 2). We can think of such biological systems as occurring at any level of biological organization, from *physiological systems,* within an individual organism, up through biological communities. In this article, we are concerned mainly with ecological--not physiological--levels of organization, and we take an individual organism and its environment, a population and its environment, and a biological community and its environment to be *ecological systems. Ecosystems* are generally taken to be biological communities together with their physico-chemical environments. There are, of course, intermediate levels of organization with which we will have to deal.

Before we move on to consider problems of creating laboratory systems at different levels of biological organization, let us emphasize general considerations applying to all levels. Laboratory ecological systems are physical-biological models. And, hence, as we noted in our earlier discussion of models, laboratory ecological systems must be evaluated in light of the *objectives* for which they are intended. Objectives of biological research must ultimately relate to natural systems. Thus, we must have some notion of the natural biological systems we intend to model in the laboratory, or we would have no way of knowing the meaning of our results or how they might be applied in reduction of problems of toxic substances in the environment.

The conceptual framework developed by Warren, Allen, and Haefner (MS) emphasizes the importance of the theoretical concept *capacity* in the explanation and understanding of the organismic part of biological systems. Capacities are specific to particular organismic systems, whatever their levels of organization. Whenever we employ organismic systems of higher than individual organism levels of organization in our laboratory studies, especially multispecies systems, we in large part determine the capacities of the systems by our design. Thus we determine possible performances. Nevertheless, we must determine or ascertain that the organismic systems we study have the capacities for the performances in which we are interested--and that the performances we measure are indeed those of the organismic system as a whole, and not just some subsystem of it. Otherwise, we had just as well study the subsystem. Organismic performances of interest may be *persistence, development, structure, replication,* or some other. In environmental toxicology, *biological magnification* (accumulation) and *degradation* of toxicants may be taken to be performances of organismic systems on different levels of organization.

Now the performances of any organismic system that we measure or might be able to measure are determined not only by the potential capacity of that organismic system but also by its environmental system in its previous as well as present states. In determining the environment of any organismic system in the laboratory, we further determine what performances will occur. Thus it is extremely important how we select the environmental factors and their levels to be employed. The behavior and effects of any toxicant will depend very much on other environmental factors and their levels. And a *range of other environmental factors* should be investigated, so as to at least partially evaluate the capacity of the organismic system of interest. This is an important way of determining the meaning and possible applications of performance results.

We can now begin with consideration of difficulties of creating laboratory biological systems at the *individual organism* level of organization, for studies in environmental toxicology. Here, the problems are mainly associated with creating the environmental part of the biological system, for an individual organism, as a whole, is in itself a *natural organismic system,* owing to reproduction, development, and evolution. But the difficulties of creating a meaningful environmental system for individual organisms in the laboratory are real enough. Let us start with *objectives* of laboratory toxicological studies of individual organisms. A common objective is to determine the relative potency of different toxic substances by employing the individual organism as a "biological reagent," in the classical sense of *bioassay*. Other than standardization of species, response measurements, and test conditions, there are no great difficulties in attaining this objective. But rational use of such information is not a simple matter. Another objective may be to determine *accumulation* or *decomposition* of toxic substances by individual organisms. And, perhaps most often in environmental toxicology the objective is to determine the *effects* of toxic substances on one or more performances of the individual organism. Because presumably these last sorts of objectives generally are ultimately related to possible effects of toxicants on species populations in nature, selection of the environmental factors and levels as well as the performances to be studied is critical. Not only selection but also creation of these conditions is difficult. But if these are not well done, the meaning and possible applications of any results are limited.

By individual organism we mean the *entire life history*, from zygote through development to reproduction and finally death. Nearly all individual organisms, as natural systems, have the *capacity* for all performances upon which this developmental trajectory depends. At this level of organization, the problem of creating a biological system in the laboratory is nearly entirely one of designing and *providing an environmental system* in which the life history can be completed. For small organisms having relatively short life histories, this can very often be done. But obviously, for many species, facilities and time alone may make this impractical. Yet, if our studies of the effects of toxicants on individual organisms are to relate, even indirectly, to the persistence of population in nature, individual organism performances of *reproduction, development, growth* and *persistence* must be studied.

Environmental Protection Agency scientists have developed and employed chronic tests in which one or more generations of species of fish or smaller organisms have been maintained in the laboratory at constant toxicant concentrations (Mount and Stephan, 1967). In determining toxic effects on entire life history sequences, such studies are well directed. But under different sets of environmental conditions, the effects of toxicants on various life history responses cannot be expected to be the same, and food availability, temperature, and many other conditions in nature vary continuously. So also do concentrations of toxicants and life history stages exposed. Obviously, all this raises very serious difficulties in designing individual organism studies so as to make the results applicable to nature. Somehow we must learn more of the *possible ranges of performances* of a kind, under various sets of environmental conditions--learn more of the effects of toxicants on the *capacities of organisms*. Much can be learned about the effects of toxicants on the capacities of individual organisms for reproduction, development, growth, and persistence by means of studies not encompassing entire life history trajectories (Warren, 1971), but such more limited studies do raise questions about what effects would have occurred if previous or later stages had been exposed.

A *biological population* is usually defined as a more or less isolated group of interbreeding organisms, there being no satisfactory definition for populations of strictly asexual organisms, of which there appear to be relatively few. As such, a population should be viewed as an organismic system on a level of organization higher than that of the individual organism. Accordingly, biological populations have capacities and performances that individual organisms do not have. These include *population growth* in numbers or biomass, *evolution*, and *persistence through many generations*. And populations exhibit some *structure* or organization: they are not simple aggregations of individual organisms. The reason for studying populations, rather than some other level of organization, is interest in population level capacities and performances. Thus, in environmental toxicology, *objectives of population studies* could be to determine effects of toxicants on population growth, production, evolution, persistence, or the capacities for these performances. Accumulation or degradation of toxicants by populations as wholes could also be of interest.

We do not, in any ordinary sense, create a biological population in the laboratory by the mere act of bringing together a group of individuals of the same species. Rather, if we are to have anything resembling a biological population, we must provide individuals with environmental conditions suitable for them to complete their life histories, including reproduction. And sufficient space and time and suitable environmental resources and conditions must be provided for growth of a population through at least several generations. During this time, the population will develop sex, age, size, and perhaps social structure. And it will come to have capacities and performances, according to the nature of the species, the genetic potentials of the original individuals, and maintained environmental conditions. For different environmental conditions, different birth and death rates will come to prevail and laboratory populations will come to have different structures. And the effects of toxic substances, as well as toxic substance behavior, will be dependent on population structure as well as on environmental conditions other than the toxicant.

Such biological populations are routinely developed in laboratories for ecological and evolutionary studies, textbooks being replete with examples. But because of time and space requirements for completion of many generations and maintaining the populations, most studies have employed small organisms having short life histories. Among animals, protozoa, insects, and small crustacea have been most studied in this way, although there have been studies on small rodents and fish as well as other groups. Studies of the capacities and performances of populations of small organisms in the laboratory could be of much more importance than they have been in environmental toxicology. There is much precedent for such studies, and a sound empirical basis, but there is also much to warn us of the difficulties inherent in their conduct and interpretation.

Here again, as with the individual organism, the difficulties center mainly around our being able to provide suitable environmental conditions for the completion of life histories. Even when this is done, and populations develop and persist for many generations, possible meanings and application of results depend nearly entirely on how well the natural environment of any studied population has been modeled. We can hardly replicate well all physical and biological conditions of a natural population's environment. We may come most near to doing so with some phytoplankton and zooplankton species and certain grain weevils. But for larger species having more complex environments, introduction of environmental factors such as several prey species, competitors, and predators in a realistic way presents serious difficulties. Nevertheless, there have been modest successes in some work of this sort, and models are always justifiably simplifications of nature. We would only emphasize one further matter: the realized capacities that develop and the performances that occur in a laboratory population are specific to the prevailing laboratory environments. We should explore population capacities and performances over as wide a range of selected environmental conditions as possible, if it is our intent, as it usually must be, to apply our results to nature. And in such exploration we must, insofar as possible, account for both time-variant and steady-state behavior of population level performances.

Possible creation in the laboratory of *multispecies ecological systems* that have level-specific capacities and performances, making them systems in their own right, presents very great difficulties. Even the results of classical predator-prey and competition studies, in which at most a few interacting species populations have been maintained in the laboratory, have very doubtful meaning and have not been related well to natural systems. At multispecies biological system levels, we not only bring forward the difficulties associated with providing suitable environments for completion of life histories and maintenance of populations--which we have at individual and population levels of organization--we have actually to compose a meaningful organismic system of two or more interacting species populations. Even if we are successful in creating a multispecies system, we in large part, by the species we bring together, determine what the capacities and thus the performances of that system will be.

We defined a *biological community*, in the organismic sense, as the *sere* composed of all successional or developmental stages of the community. We suppose such high-level organismic systems to exist in nature, or we would have little reason to talk of them. On the basis of this supposition, biological communities must have level-specific capacities and performances, however well we are able to observe them. The major performances of a biological community can be taken to be *development* (or succession), *structure*, and *persistence*. The *effects of toxic substances* on any of these can have serious implications for man. And *movement, accumulation, and degradation* of toxic substances by biological communities is also a matter of great concern, one that has led to many studies employing laboratory models.

Our reasons for studying a particular level of biological organization presumably are based on interest in capacities and performances of systems having that level of organization. Very few if any laboratory systems can be believed to represent ecosystems, for this implies that biological communities, with all their complexities, capacities, and performances have been created. Many attempts, with some success, have been made to create multispecies systems for toxicological studies in the laboratory, most of which have involved relatively few species and certainly can represent, at most, very low levels in community organization.

One objective of multispecies systems studies in environmental toxicology is *assay of the relative toxicity* of substances. There is, however, considerable difficulty in experimentally replicating multispecies systems in a way that would be necessary for them to serve as "reagent" organismic systems for assaying the relative toxicities of substances.

The major objective of most of the published work employing multispecies systems in environmental toxicology has been determination of *transport,* *distribution*, and *degradation* of toxic substances. Metcalf, Sangha, and Kapoor (1971, p. 709, p. 711) state: "We need a realistic laboratory method for screening proposed new pesticides for their environmental fate." And, "The ultimate purpose of the model ecosystem is to be used as a single living unit for in-depth studies of environmental biodegradability." Isensee and Jones (1975, p. 668), with respect to their laboratory ecosystem, note: "This system is not designed to determine the effects of a chemical on the organisms (though some primary effects can be assessed) but rather, how does the chemical behave when subjected to likely environmental conditions." And Gillett and Gile (1975, p. 1) state that "The need to know or project accurately potential effects of chemicals deliberately or accidentally added to the environment forms the basis for the development of laboratory ecosystem simulators."

In our own laboratory we have used simple multispecies systems to evaluate the effects of such factors as temperature, dissolved oxygen, ammonia, pulp and paper industry effluents, and other toxic materials on the behavior, food utiliztion, growth, development, and survival of individual fish. The use of multispecies systems for this purpose permits evaluation of the performance and capacity of individual organisms under conditions perhaps more like those in nature than are usually provided in simple aquarium studies. In many cases, but not always, these studies have been a part of broader investigations directed toward effects on populations and on the multispecies systems as wholes.

Among others, Taub (1973) has conducted multispecies system studies having the objective of evaluating direct and indirect effects of toxicants on populations of algae and *Daphnia*. Some of our own studies on fish population in laboratory stream systems have had the objective of determining direct and indirect effects of various toxic and other environmental changes not only on the production of populations but also on the capacities of biological systems to produce them. These studies have in some cases been directed toward determination of the effects of environmental changes on the persistence, development, and structure of laboratory communities as wholes (Warren and Davis, 1971). Such community-level objectives have been implicit in studies of other investigators.

The laboratory systems developed by Metcalf (1974) and his colleagues (Metcalf, Sangha, and Kapoor, 1971, and many papers following this one) are designed primarily to evaluate accumulation and degradation of toxic substances. These systems are contained within glass aquaria measuring 10 x 12 x 20 inches and illuminated with 5000 ft candles of light 12 hours each day. Sand is formed into a sloping surface and a standard water added so as to represent both terrestrial and aquatic habitats. After 1 day, *Sorghum halpense* seeds are planted, and 10 *Physa* snails, 30 *Daphnia magna*, and a few strands of the alga *Oedogonium cardiacum* are introduced. In 20 days, when the *Sorghum* plants have reached about 4 inches in height and are treated with radiolabeled pesticide, 10 larvae of the salt marsh caterpillar, *Estigmene acrea* are added. On the 26th day, 300 larvae of the mosquito *Culex* *pipens quinquefasciatus*, and on the 30th day 3 mosquito fish, *Gambusia affinis* are introduced to complete the laboratory model. The mosquito fish readily consume all remaining *Daphnia* and mosquito larvae, and the experiment is terminated at the end of 33 days. Samples of sand and water are collected periodically during the experiment and biological materials are collected at the end of the experiment for analysis of concentrations of the introduced toxic compound and its metabolites.

Isensee and his colleagues (Isensee, Kearney, Woolsen, Jones, and Williams, 1973) have designed and employed laboratory models essentially like those of Metcalf except that no terrestrial phase has been provided. Aquaria holding 4 liters of water were kept in a greenhouse at about 22 C. *Daphnia*, *Oedogonium*, and *Physa* were first introduced. After 29 days, by which time the *Daphnia* were found to have increased from about 30 to 100, 2 mosquito fish were added to each of the aquaria. The experiment was terminated 3 days later, after the fish had consumed all the *Daphnia*. Toxic substances were introduced either directly into the water or first adsorbed onto soil that was added. Analyses for concentrations of these substances in water and organisms were made during and at the completion of the experiments.

Gillette and Gile (1975) have developed quite elaborate physical systems for containing terrestrial organisms and controlling environmental conditions. Air flow and humidity can be controlled and water is provided by a sprinkler system and a "spring" system. Light intensity is controlled even to the extent of providing short "dawn" and "dusk" periods, and there is careful monitoring of temperature at various points within the chambers, which are in a temperature controlled room. The chambers themselves are 1 meter long and 0.75 meter wide. A considerable variety of plant and animal species is maintained in these terrestrial laboratory models, including the vole *Microcaudus canicaudus* and the quail *Excalfactoria chinensis*, food for which had to be supplemented. By the end of an experiment, 30 to 45 days, "The pregnant female vole literally destroys the terrarium." Cole, Sandborn, and Metcalf (1976), who included the vole *Microtus ochrogastu* in a terrestrial model with corn plants and other organisms during the last 5 days of an experiment, noted that "it is not uncommon to find that all other organisms of the system have been consumed" by the vole.

Now, before we go on to review the design of laboratory models employed in studies having other objectives, let us only in very general terms evaluate the designs of multispecies systems directed toward determination of the transport, accumulation, and biodegradation of toxic substances. The sorts of laboratory models we have just characterized do not satisfy the rather severe criteria for organismic and environmental systems that we have argued should be met if we are indeed to have multispecies laboratory systems. The species of organisms included in these laboratory models are not adapted to one another so as to lead to the development of multispecies systems capable of persisting under the environmental conditions provided. The scientists employing these laboratory models are generally aware of this. This awareness is implicit in the experimental protocols in which fish or voles are introduced into the models only during the last few days of experiments, the models not having the capacity to support these vertebrates for much longer. The awareness is repeatedly made explicit in comments to the effect that the fish or the voles consume all their food organisms in a few days. Even in the larger and more productive biological model developed by Gillett and Gile (1975), supplemental feeding was necessary to maintain the quail, and in 30 to 45 days single voles were noted to have destroyed the plants and animals in their environments. These laboratory models, at least so long as the vertebrates are included, are not persistent systems and may not reflect reliably the behavior and effects of toxic substances in natural systems.

One of the major reasons systems having some capacity for persistence under provided environmental conditions have not been created is failure to insure that, at each step or link in a food chain or web, sufficient energy and material resources will be available. For the plant trophic level, sufficient light energy and nutrients must be provided not only for plant maintenance but also for plant growth adequate to provide energy and materials for succeeding trophic steps. And at each of these succeeding steps, the animals selected for inclusion must be capable of producing enough material under prevailing conditions to support those following. Ideally, both reproduction and growth capacities and performances of included organisms should be sufficient to support other organisms depending upon them; but multispecies systems can sometimes be designed so as to persist for useful periods of time mainly on the basis of the growth and production of their organisms. But neither growth nor reproduction of food chain organisms will be adequate to support larger animals such as fish, birds, and voles in laboratory models having such small physical dimensions as we have considered, available light energy and plant production being too low for this. Rather large and carefully designed laboratory ecosystems are necessary if large animals are to be sustained.

We wonder if the kind of information on behavior and effects of toxic substances obtained from short-term studies of nonpersistent systems cannot be obtained more simply and comprehensively from studies of individual organisms or groups of individual organisms of the same species. Individual organisms can more simply be held in toxicant contaminated medium and fed contaminated food organisms than in even partially self-sustaining systems. Survival, growth, and even reproduction rates as well as accumulation and degradation can be determined over a wider range of toxicant concentrations and energy and material utilization rates. Thus lethal and sublethal toxicant effects and accumulation and degradation can be evaluated and interrelated. Good information of this sort can be incorporated into theoretical deductive systems and models and so be extended to prediction of multispecies system effects, perhaps more reliably than prediction can be made from all but the most sophisticated laboratory ecosystems.

Let us now move on to consider laboratory model studies having somewhat different objectives. The work of Taub (1973) and her colleagues on algae and protozoa, which we considered earlier, is exemplary in complementing well-designed studies of multispecies systems with generalization by means of a reasonably adequate simulation model (Fig. 13). Work of this sort amounts to a rather extensive exploration of the theoretical capacity of a biological system. Introduction into this system of a toxicant affecting either or both the alga and the protozoan would have altered the scope for performance of the system as a whole and the domains of steady states under different environmental regimes.

Many of our own studies employing laboratory systems have had the objective of determining the effects of toxic substances and environmental factors on the capacity of these systems to produce products of interest, especially salmonid fishes. We began laboratory stream community studies about 20 years ago and were soon able to maintain groups of salmonids feeding on insects and other invertebrates produced in these streams for periods as long as we might wish, although only a few experiments were allowed to continue for more than about 6 months. But even though these were moderately persistent systems having capacities and exhibiting performances in which we were interested, they did not entirely satisfy our criteria for multispecies laboratory ecosystems. In particular, completion of trout life histories requires two or more years, and anadromous salmon must go to the sea and return before reproducing. Because of the importance of reproduction in determining the persistence, production, and yield of fish populations exposed to toxicants, we began studies with guppies, a fish species capable of reproducing fairly rapidly in the laboratory.

Some studies were directed toward evaluation of the effects of dieldrin on the age-specific fecundity and survival of individual guppies, such information making it possible to theoretically determine effects on the capacity of guppy populations to increase in number (Roelofs, 1971). Laboratory population studies with guppies were conducted by Liss (1974). He maintained populations of guppies for 15 consecutive months and exploited them at different rates up to 60 percent per month to determine the effects of dieldrin on population biomass, number, and yield to exploitation. Biologists at our laboratory are now evaluating the effects of dieldrin on the structure and persistence of multispecies systems composed of populations of guppies, amphipods, copepods, and other invertebrate species. The guppy populations in these systems are being subjected to different rates of exploitation. To insure persistence of the systems prior to introduction of toxicant, invertebrate prey species that could support guppy populations had to be found and an adequate food supply and protective habitat for the invertebrates had to be developed. These systems have been in operation for one year.

In the 1950's we began studies on the effects of pulp and paper mill effluents on organisms in laboratory streams. It soon became apparent to us that we did not understand laboratory stream communities well enough to be employing them in the evaluation of toxic materials. Thus, we discontinued such evaluation and undertook several years of study on the dynamics and productive capacity of laboratory stream communities including bacteria, algae, insects, and other invertebrates, and different species of fish (see Warren and Davis, 1971, for a review).

Only after we had achieved a reasonably good empirical understanding of these systems did we return to the problem of evaluating the effects of pulp and paper industry effluents on the structure, dynamics, and fish productive capacity of laboratory stream communities. Results of this work made it possible for us to estimate very closely those concentrations of pulp and paper industry effluents which did not decrease fish production in large outdoor stream channels (Warren et al., 1974). Our own experience, then, has been that it is important to achieve good understanding of laboratory systems before employing them in evaluation of complex environmental problems.

On the basis of this understanding, we have evaluated the effects of temperature, dissolved oxygen, chloramines, pesticides, and heavy metals as well as pulp and paper industry effluents on community structure and the capacity of these systems to produce fish (Warren, 1971; Warren and Davis, 1971; Bisson and Davis, 1976; Seim et al. 1977). But generalization of the findings of such empirical investigations so as to apply them with more confidence to the natural systems where the problems occur requires adequate conceptual structures. Limitations of the applicability of our empirical investigations convinced us of the need for conceptual frameworks and theory.

B. EMPIRICAL DETERMINATION OF ORGANISMIC SYSTEM PERFORMANCES

All we can ever observe or measure, however directly, are *particular performances* of organismic systems, whatever may be their levels of organization. All else we attribute to systems or their performances by means of conceptual structures of various kinds and degrees of abstractness, generality, and invariance (Fig. 1). We cannot observe the capacities of natural systems, nor their operation, nor their functions or purposes. On this, important philosphers agree. But they also agree on the importance and pragmatic rationality of so conceiving of systems that we can explain them in these ways, thus making understanding possible. Perceptual experiences--the system performances we observe--are in continuous flux. Such experience, in itself, has no meaning--is not understandable. We try to find general and invariant ways--universal ways--of making perceptual experience understandable. Environmental toxicology cannot escape this imperative. Otherwise, it cannot give meaning to its empirical results and thus cannot reliably apply these to solutions of potentially very serious problems of toxic substances in man's environment.

In this section, we intend to say something of the performances we observe, the levels of system organization with which they appear to be associated, and the problem of giving meaning to or understanding observed performances so as to know something of their generality, invariance, and possible application to problem solution in environmental toxicology. In the next section, we will consider the empirical evaluation of capacity, a very partial and yet effective approach to determination of the domain of applicability of performance measurements.

First, it is important that we know, insofar as possible, the level of organization having the performance we are interested in and intend to measure. For laboratory research, failure to associate performances with the organizational level from which they derive may lead to attempts to create far *more complex systems than necessary* to obtain desired performances, to incorrect interpretation and application of results, and to loss of opportunity to more adequately evaluate the capacity of the subsystem actually having the performances of interest. We have considererd organismic systems at the individual, the population, the multispecies system, and the community levels of organization, though we have concluded that little can adequately be done in the laboratory at a level of the biological community. For the *individual organism*, development, growth, reproduction, and persistence are major performances that can be determined. *Population performances* are growth (change in number or biomass), structure, evolution, and persistence. And *multispecies systems* may exhibit some sort of development, as well as structure and persistence. But there are real difficulties in interpreting single or even series of performances of systems on any of these levels of organization. Let us expand on this topic only for one sort of performance, say growth, at the individual level of organization: the same problems of interpretation exist for any performance of any organismic system on any level of organization.

Now were we to have an individual organism in the laboratory, under a given set of environmental conditions and fed a given amount of food, we could measure its growth. The particular growth performance measured could be "explained" as a result of the food eaten under the prevailing set of environmental conditions. But what more could we say? We know that, in all probability, had the amount of food or the quality of food fed been different, the growth performance measured would have been different. Moreover, had any important factor in the set of environmental conditions been at a different level, the growth performance would probably have been different, even for the given amount and quality of food. And had the animal been at a different size or stage in its life history, all else being the same, the measured growth performance would have been different. Or had the animal been exposed to some different set of environmental conditions before the growth experiment began, still all else being the same, it is quite likely a different growth performance would then have been measured. There is virtually nothing of a general and invariant sort that we can say about a single measurement of performance. *We do not know how to apply such a result to nature, where we know environmental conditions are different and in continuous flux.*

This simple and obvious example is perhaps trivial. And yet it pertains to all single measurements of performance of any organismic system whatsoever. Moreover, the problem is compounded when we attempt to interpret single measurements of performance of organismic systems on levels of organization higher than the individual. We want and indeed need to be able to apply our laboratory results to the solution of problems in environmental toxicology. But this cannot reliably be done with single measurements of performances under given conditions, no matter the complexity of the systems we study. Indeed, the very complexity of the systems we study may delude us into believing our measurements of performance are more significant than we have any reason to believe.

Perhaps we should further note that, were we to be studying the effects, accumulation, or degradation of a toxicant in an experiment something like the one described, a single measurement of any of these under any of the fixed conditions would have no more meaning than a single measurement of growth performance. For changes in rate of food consumption and in environmental conditions would change the metabolic state of the organism, the opportunity for accumulation of the toxicant, and probably effects, accumulation, and degradation of the toxicant. And all such changes would carry through to affect related performances of higher level systems, were the individual organism to be a part of these.

The results of an experiment conducted by Morgan (1972) on the effects of Arochlor 1242 on population growth of a species of algae are presented in Figure 14. We introduce this here to illustrate, for a population level performance, the importance of successive measurements over a sufficient period of time when time-variant performances are being evaluated. Had measurement of the density of each population been only at day 3, day 10, day 15, or day 22, one would reach different conclusions on the effects of this toxicant on population growth, under the experimental conditions. But because Morgan, through a series of measurements, determined the time trajectories of population growth, much more complete interpretation is possible. The effects of the toxicant on population density was time variant until equilibrium conditions were reached. Had this been an open system providing continuous renewal of nutrients at different concentrations and perhaps removal of algal cells, or had light or temperature conditions been different, time-variant and equilibrium densities and observed effects of the toxicant would in all probability have been different. This experiment is a partial evaluation of population capacity for growth in the presence of a toxicant. Even so, population performances would need to be determined under a wider range of conditions, if the results were intended to relate reliably to possible effects of the toxicant in nature.

The behavior and effects of chlorinated hydrocarbon pesticides introduced in natural and cultural ecosystems have provided much empirical basis for concern abut the possible persistence and accumulation or degradation of toxic substances employed by man. The emphasis of much of the work directed toward evaluation of transport, accumulation, and degradation of such substances has been on estimation of ecological magnification and biological degradability indices. The *ecological magnification index* is generally defined as the ratio of the concentration of a substance in any biological element of a system to that present in water or soil, although *partial indices* may be defined as the ratio of concentrations between any two elements in a system transport pathway. The *biodegradability index* is generally defined as the ratio of the concentration of polar metabolites to that of the remaining parent compound, this ratio being determinable for an individual organism, a population of organisms, or a

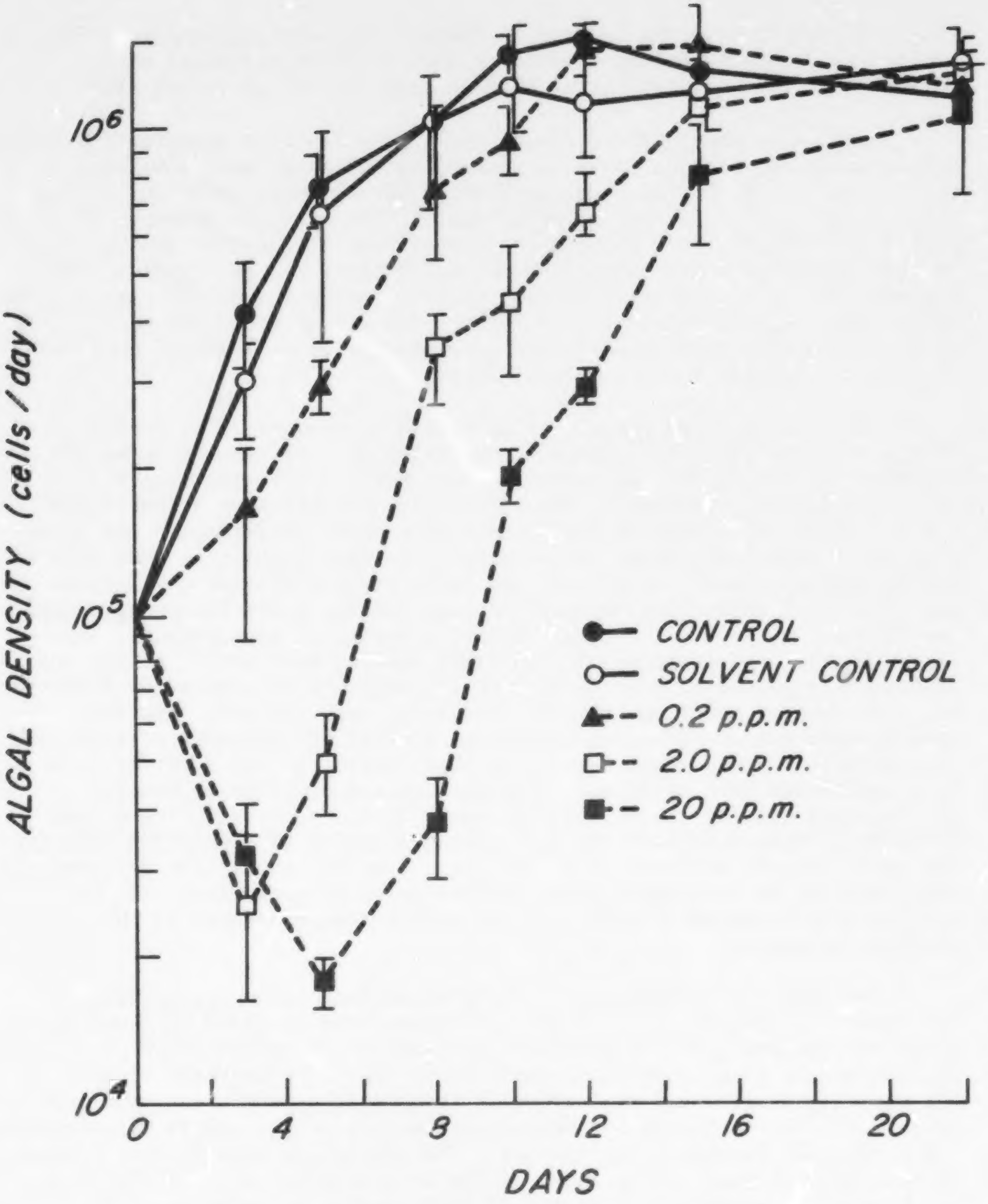

Figure 14. Effects of the addition of 0.2, 2, and 20 ppm Aroclor 1242 on the growth of *Chlamydomonas reinhardtii*. Each point represents the mean of two observations whose individual values are indicated as the range. After Morgan (1972).

laboratory ecosystem as a whole. Accordingly, the values obtained for either of these indices will be dependent on just what level of system organization is included in their definition. Gillett and Gile (1975) suggest that persistent--and implicitly destructive-- toxicants have, on the basis of field studies, ecological magnification indices usually greater than 1,000 and biodegradability indices usually less than 0.5; whereas presumably less harmful toxicants have ecological magnification indices usually less than 100 and biodegradability indices usually greater than 1. Much of our concern must, then, be with the reliability and generality of estimates of ecological magnification and biological degradation indices obtained from laboratory systems, and with how reliable these indices may be in identifying actually or potentially harmful compounds.

As we have stated earlier, by design we determine the capacities and thus the possible performances of multispecies laboratory systems. Levels of all performances, including accumulation and degradation, will be dependent upon the species included in the system and their interactions, the state of the system including levels and rates of utilization of energy and material resources, the metabolic states of the organisms, and the levels of environmental factors, including toxicant concentration, that are being tested. In Table 1, some examples of the differences in ecological magnification indices obtained from systems with different designs and experimental protocols are presented.

Others have noted various aspects of the difficulties to which we allude. Matsumura and Benezet (1973) state that: "It is apparent from these data that the reaction of biological concentration is greatly influenced by the external conditions and the design of the experiment, the physical and biological nature of the organisms, and the chemical characteristics of the pesticide." Isensee et al. (1973) note that: "Use of nonrepresentive rates [of toxicant introduction] may result in erroneously high or low bioaccumulation ratios which would be of no value in extrapolating laboratory results to actual environmental conditions." And Isensee and Jones (1975) state that: "The bioaccumulation ratios obtained in this study were higher than the concentration factors obtained by Matsumura and Benezet (1973). However, the experimental conditions used in the two studies were considerably different--i.e., we used a longer exposure time, different organisms, a larger system design, and a wider range of water concentrations."

This raises the problem of what designs, protocols, and conditions are sufficiently general to provide reliable estimates upon which to base important decisions pertaining to the use of toxicants. Furthermore, for a system of a particular design, we believe it is important to evaluate the performances of the system, including transport and accumulation, over a range of environmental conditions--to explore the domains of system and subsystem performance--if we are to apply our results with any confidence to nature. We will discuss this in more detail in the following section.

Finally, transport, fate, and degradation of toxic substances are important in explanation and understanding of effects of toxicants on natural systems, but ultimately it is effects that must concern us. *Single estimates of ecological magnification or biodegradation cannot possibly account for the numerous kinds and magnitudes of effects of toxic substances on complex biological systems.*

CHEMICAL	ECOLOGICAL MAGNIFICATION					REFERENCES
	Algae	Daphnia	Mosquito	Snail	Fish	
DDT			16,765;21,571		218;306	Matsumura and Benezet, 1973 (Aquatic systems)
			8,182		84,500	Metcalf, 1974b(Terrestrial-aquatic systems)
Dieldrin	7,480			114,935	6,145	Sanborn and Yu, 1973 (Terrestrial-aquatic systems)
	457			61,657	2,700	Metcalf, Kapoor, Lu, Schuth, and Sherman, 1973 (Terrestrial-aquatic systems)
Hexachlorobenzene	3,969	1,129	2,622	2,672	1,166	Lu and Metcalf, 1975 (Aquatic systems)
	522	201	144	1,247	287	Metcalf, Kapoor, Lu, Schuth, and Sherman 1973 (Terrestrial-aquatic systems)
Dioxin		49;2198			54	Matsumura and Benezet, 1973 (Aquatic systems)
		7,800-48,000			1,000-63,300	Isensee and Jones, 1975 (Aquatic systems)
						Lu, Metcalf, Hirwe, and Williams, 1975
Chlordene				4,167	465	Aquatic systems (3 day test)
				53,038	1,122	Terrestrial-aquatic systems (33 day test)
Heptachlor				1,841	1,143	Aquatic systems (3 day test)
				37,153	3,820	Terrestrial-aquatic systems (33 day test)
Heptachlor epoxide				2,781	1,324	Aquatic systems (3 day test)
				66,462	4,888	Terrestrial-Aquatic systems (33 day test)

Table 1. Ecological magnification indices (concentration of chemical in organism/concentration of chemical in water) obtained from laboratory multispecies systems having different designs and experimental protocols.

C. EMPIRICAL EVALUATION OF ORGANISMIC SYSTEM CAPACITIES

We have been leading, from conceptual framework considerations through theoretical considerations and now through empirical considerations, to the fundamental importance of capacity to organismic systems and our explanation and understanding of them. In presenting our conceptual framework, we endeavored to make clear our abstract concepts of *potential capacity* and *realized capacity* of organismic systems for performance. Then, with isocline theory, we attempted to theoretically show how organismic system characteristics determine the domain of environmental dimensions and values within which an organismic system can perform and persist, and how this domain might be influenced by introduction of a toxicant. And we have just completed consideration of the very limited meaning that can be given single empirical determinations of performances, even steady-state ones.

Now we must consider how and to what extent we can hope to empirically evaluate the capacities of organismic systems for performance. The very nature of our notion of *potential capacity*--all possible performances in all possible environments--and our notion of *realized capacity*--all possible performances at any state of the organismic system--make clear that neither theoretically nor empirically can we fully and directly evaluate either the capacity of a natural system or the capacity of a laboratory system (Fig. 15). But the fundamental importance of capacity to organismic systems and our explanation and understanding of them demand evaluation of capacity to the extent possible.

We will begin by making a *clear distinction* between our abstract *concept of capacity* and a theoretically or empirically determined *scope for performance*. We will take scope for performance to be a series of performance values determined over a series of values of selected environmental variables. *Thus scope for performance, so defined and determined, is an indirect and very partial evaluation of capacity of an organismic system.* In principle, such scopes for performance are determinable for organismic systems from physiological to community levels of biological organization. In practice, this can usually be done most adequately for individual organisms. We will begin with consideration of empirical determinations of scope for performance of *individual organisms*.

Were we to think of the total rate of energy metabolism by an individual organism to be a performance of that organism as a whole, then we could define *metabolic scope for performance*. F. E. J. Fry (1947) defined (metabolic) scope for activity as the difference between the active and resting metabolic rates of an animal under given environmental conditions. In scope for metabolic performance, we extend his meaning to include the series of differences between active and resting metabolic rates over a series of values of selected environmental variables. Fry's way of *classifying environmental factors* into controlling factors (i.e. temperature), limiting factors (i.e. oxygen), and stressing factors (i.e. toxicants) could prove to be a very powerful way of determining principles of environmental effects on organismic system capacities, without our

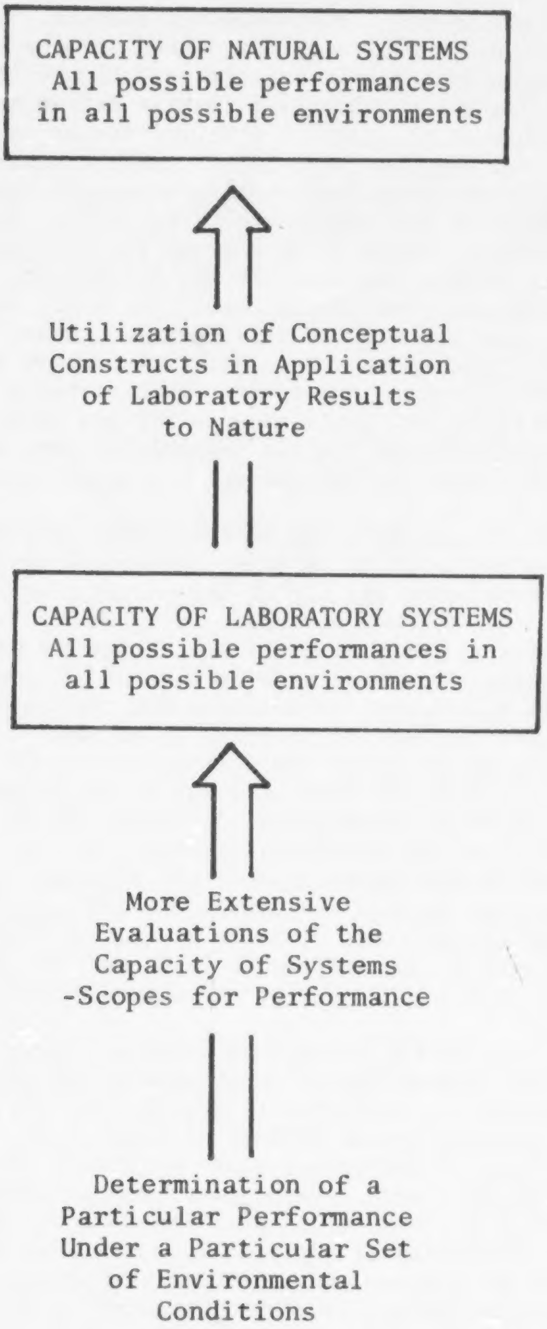
CAPACITY OF NATURAL SYSTEMS
All possible performances
in all possible environments
Utilization of Conceptual
Constructs in Application
of Laboratory Results
to Nature
CAPACITY OF LABORATORY SYSTEMS
All possible performances in
all possible environments
More Extensive
Evaluations of the
Capacity of Systems
-Scopes for Performance
Determination of a
Particular Performance
Under a Particular Set
of Environmental
Conditions

Figure 15. Diagrammatic representation of theoretical and empirical partial evaluation of capacities of laboratory ecological systems by determination of scopes for performance as sets of performances under different environmental conditions.

having to study all possible environmental factors. Determination of scope for performance has already been shown to be a very useful partial evaluation of organismic system capacities. Figure 16 illustrates how metabolic scope for performance is primarily determined by a controlling factor, temperature (Fig. 16A). A limiting factor, oxygen, would reduce scope and shift the maximum (Fig. 16C). And a stressing factor, for example some toxicant increasing resting metabolic rate, could further reduce metabolic scope for performance (Fig. 16D). Now any one of the shaded areas shown in Figure 16 is a scope for performance over the ranges of environmental factors for which it was determined. All of these scopes, along with all performance levels involved, are implicit in and a part of the *realized capacity* of any organism. Under other environmental conditions, other performances and scopes could have been determined, all a part of realized capacity. And if the organism had a different previous environmental history, its realized capacity and determined scopes for metabolic performances would in all probability have been somewhat different: hence the need for the concept *potential capacity* (Fig. 3).

Warren and Davis (1967) and Warren (1971) extended Fry's (1947) meaning of scope for activity to *scope for growth performance*, this requiring the development and use of bioenergetic concepts we need not go into here. For even without doing so, we think the different shaded areas in Figure 17 illustrate sufficiently how changing temperature and food availability determine the scope for growth of an animal. In the context of environmental toxicology, there are a few pertinent matters we should emphasize. Were a toxicant to be added as an additional environmental factor, according to its level and mode of action, it could alter metabolic state, food consumption, or food utilization for growth. And such effects could be expected to be different at different levels of food availability, temperature, or other environmental factors. We, at least, would also expect accumulation and degradation of the toxicant to be altered not only by its concentration in food and medium but also by other factors. In the time-variant and steady-state behavior of multispecies systems, changing actions and effects at the individual level must be involved. But it is not clear to us that this is always taken into consideration.

For the level of the *individual organism*, there exists an extensive literature on the interaction of environmental variables, including toxicants, on scopes for survival, development, growth, and reproduction. We would only note that information on effects of interacting environmental variables on entire life history trajectories of particular species has received very little attention, with some noteworthy exception. Much of the best of this literature pertains to insects (Andrewartha and Birch, 1954). Because of the difficulty of empirically evaluating the effects and behavior of toxicants in populations and multispecies systems we must find better ways of relating individual level performances to their possible effects on the capacities and performances of higher level systems (Fig. 4).

Most of the literature on scope for survival of individual organisms, as series of survival performances under different environmental conditions, has perhaps understandably been under acute rather than chronic conditions, especially when toxicants have been evaluated (Fig. 18). For understanding

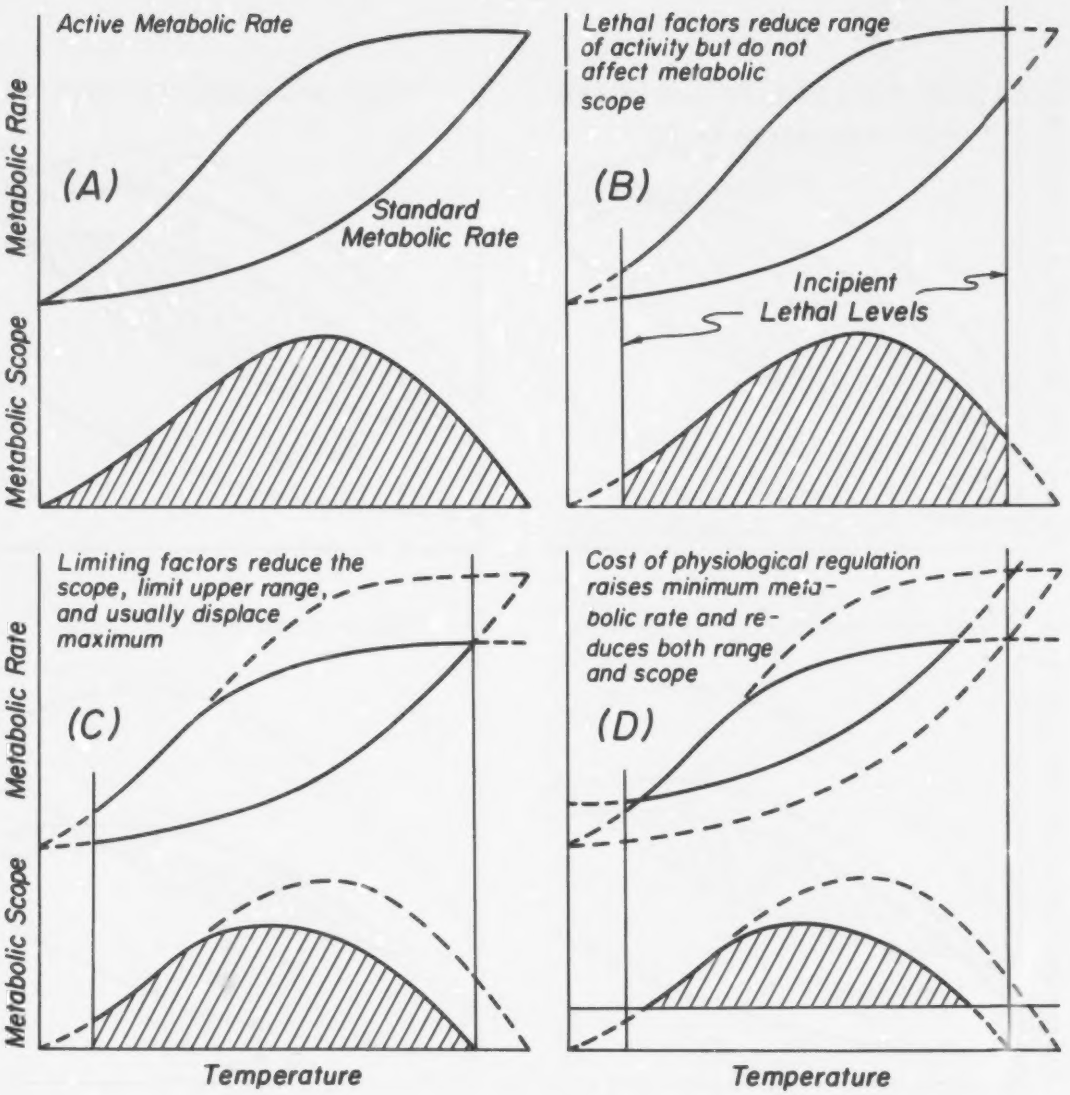
Active Metabolic Rate
Metabolic Rate
(A)
Standard Metabolic Rate
Metabolic Scope
Lethal factors reduce range of activity but do not affect metabolic scope
(B)
Incipient Lethal Levels
Limiting factors reduce the scope, limit upper range, and usually displace maximum
Metabolic Rate
(C)
Metabolic Scope
Temperature
Cost of physiological regulation raises minimum metabolic rate and reduces both range and scope
(D)
Temperature

Figure 16. The influences of a controlling factor such as temperature (A), lethal levels of the controlling factor (B), a limiting factor such as dissolved oxygen (C), and the cost of additional physiological regulation as might be caused by a toxicant (D) on the active and standard metabolic rates and on the metabolic scope for performance of a hypothetical poikilothermic animal such as a fish. After Fry (1947).

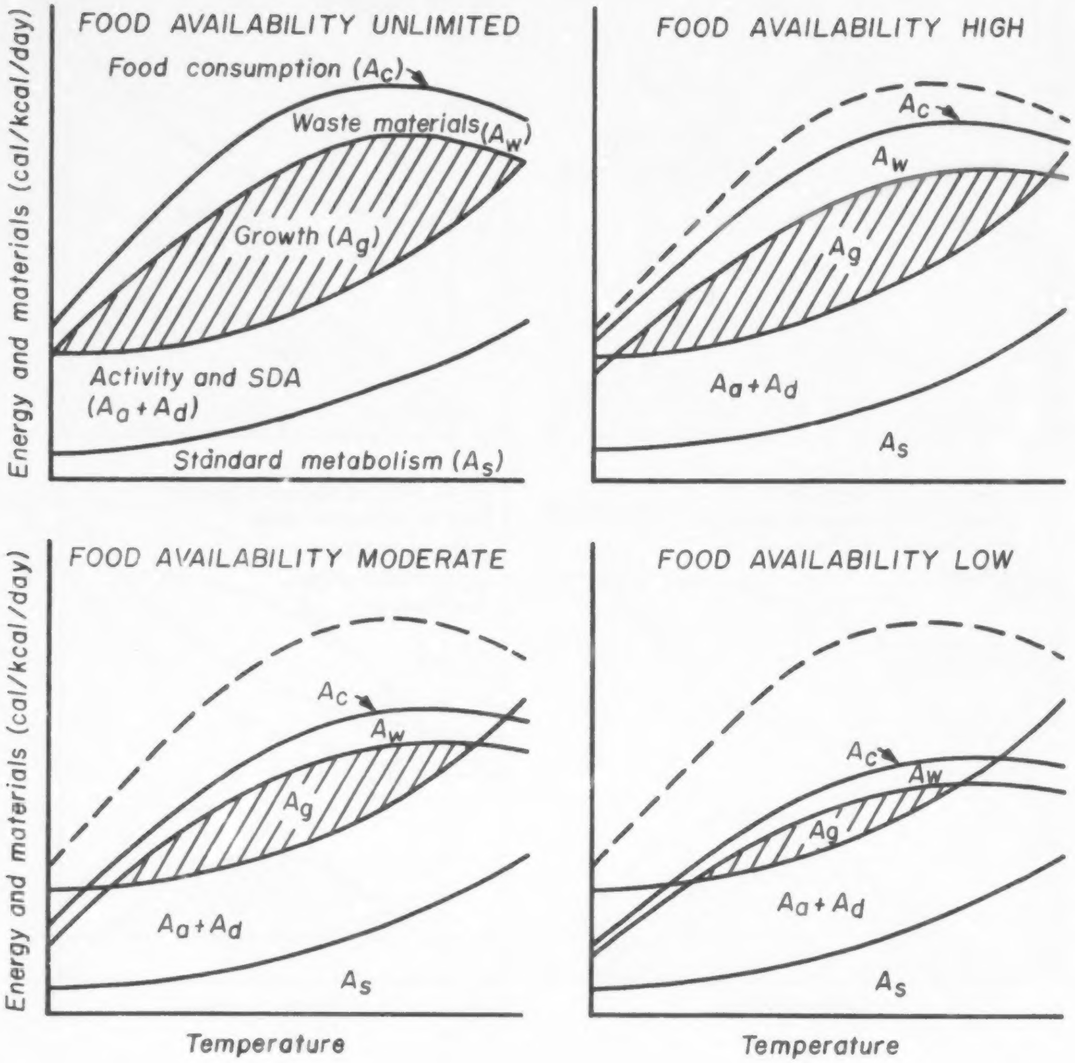

Figure 17. Theoretical effects of temperature change on the food consumption, energy budget, and scope for growth performance of a hypothetical poikilothermic animal having food available in different amounts. After Warren (1971).

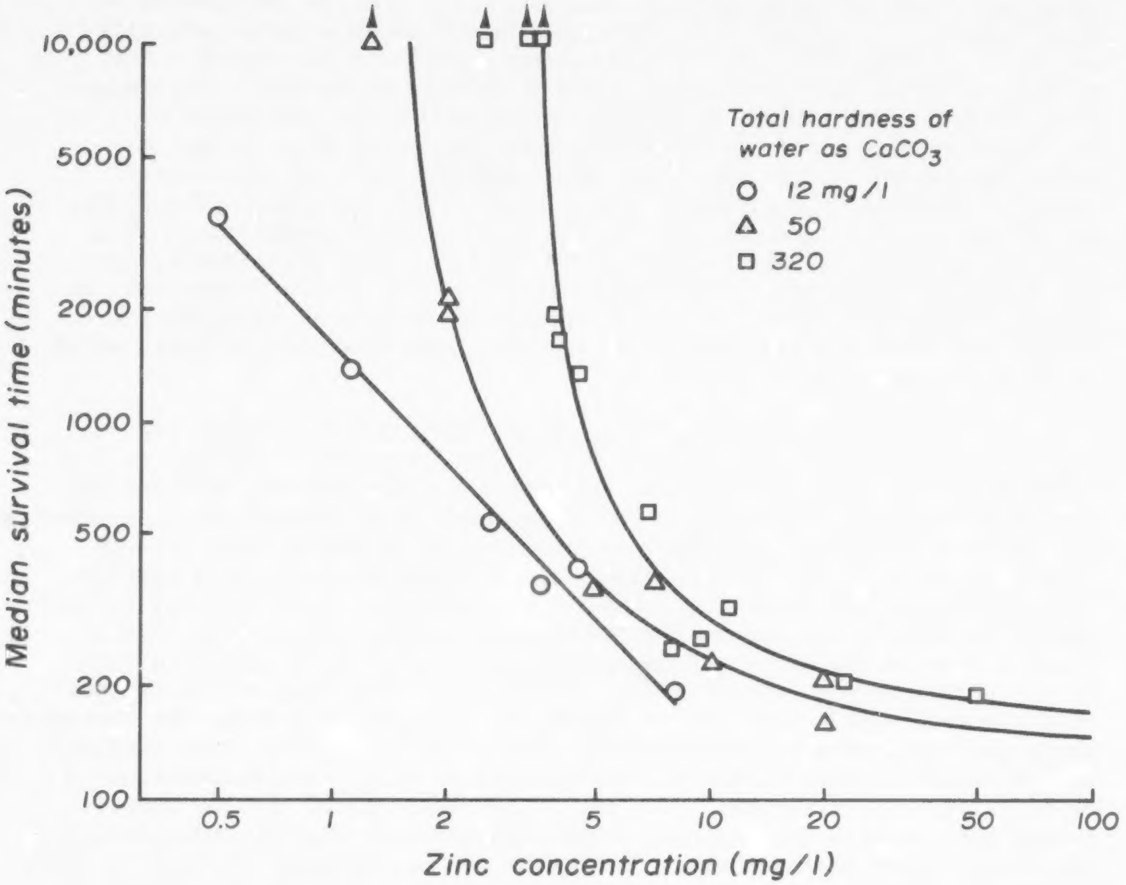

Figure 18. Relationships between median survival time of rainbow trout and concentration of zinc ion in water having different total hardness. After Lloyd (1960).

problems of this sort in nature, such work is very important, but the effects of toxicants and their interactions with other environmental factors under acute conditions cannot generally be extrapolated to include chronic conditions, which probably present the most general problem. Many studies that have provided valuable information on the effects of interacting environmental variables on the scope for survival of organisms at different life history stages, such as shown in Figure 19 for crab larvae, ought not to be ignored in empirical and theoretical consideration of problems associated with toxic substances. For, even in the absence of toxic substances introduced by man, animals are perhaps quite generally, at one or another life stage, living under conditions of limitation or stress, as we believe developing salmonid embryos to be (Fig. 20). *Under such conditions of stress, we should expect relatively low levels of toxicants to decrease scope for performance much more than we observe under the generally otherwise favorable conditions of toxicity experiments.* Toxicants can certainly decrease the scope for growth of animals, but factors such as temperature (Fig. 21) and oxygen concentration (Fig. 22), so important in determining growth in the aquatic environment, are not usually introduced as additional variables in toxicity experiments on growth. Moreover, the effects of toxicants as well as temperature and oxygen on growth are very generally a function of food availability, which is rarely considered.

The effects of toxicants on survival, development, growth, and reproduction of individual organisms must generally affect the scopes for performance of their populations, although the relationships involved are extremely complex. *Population growth in numbers,* for example, is determined not only by individual *fecundity* and *survival* in different life history stages but also by the *age structure* of a population, which is a complex function of the two individual kinds of performance. With constant environmental conditions and exponential population growth, populations *theoretically* come to *stable, or steady-state, age distributions* characteristic of particular sets of environmental conditions. This theoretical proposition has been widely employed in evaluation of population scope for increase under different sets of environmental conditions (Fig. 23). Unfortunately, we can rarely if ever expect the assumptions on which this proposition is based to prevail in nature. Even so, it provides one of the few quantitative ways we have for thinking about relationships between individual and population level performances. So long as the assumptions are kept in mind, toxicity studies could well take advantage of this approach to evaluation of population capacity for increase, much as Roelofs (1971) did for effects of dieldrin on the guppy.

The *yield* of exploited fish populations to man is another population level performance all too generally affected by man's indiscriminate use and wasting of toxic materials. Silliman (1968), with experimental guppy populations, showed how *equilibrium yield curves* are dependent upon food resource availability for the exploited population (Fig. 24). Equilibrium yield curves as well as recruitment and production curves have been shown to be determined by energy pathways, competition, temperature, toxic substances, and other dimensions of the *productivity* of the system (Warren, 1971; Liss and Warren, MS).

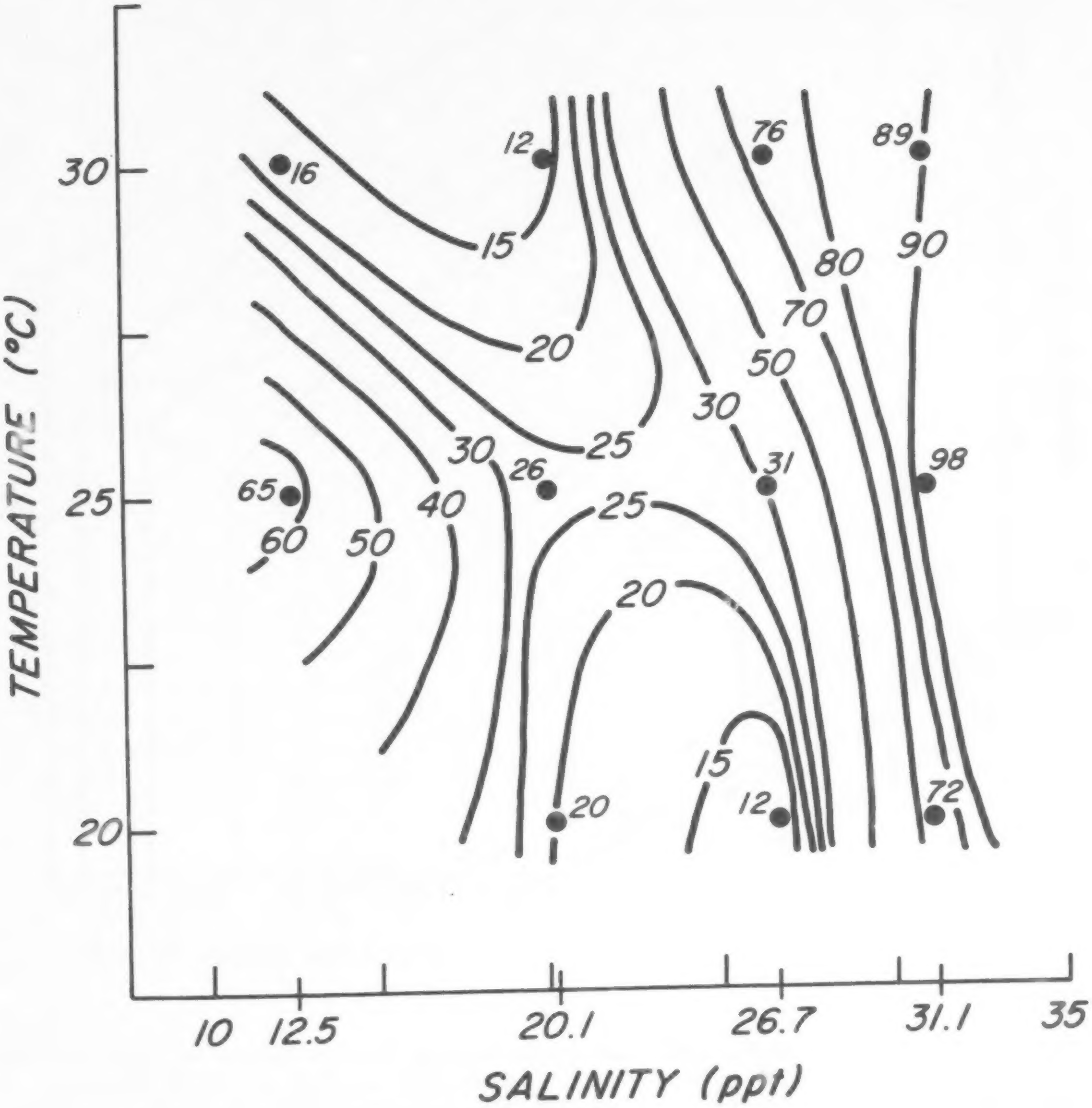

Figure 19. Percentage isopleths representing scope for survival of the fourth zoeal stage of larvae of the crab *Sesarma cinereum* in relation to temperature and salinity of water. After Maguire (1973).

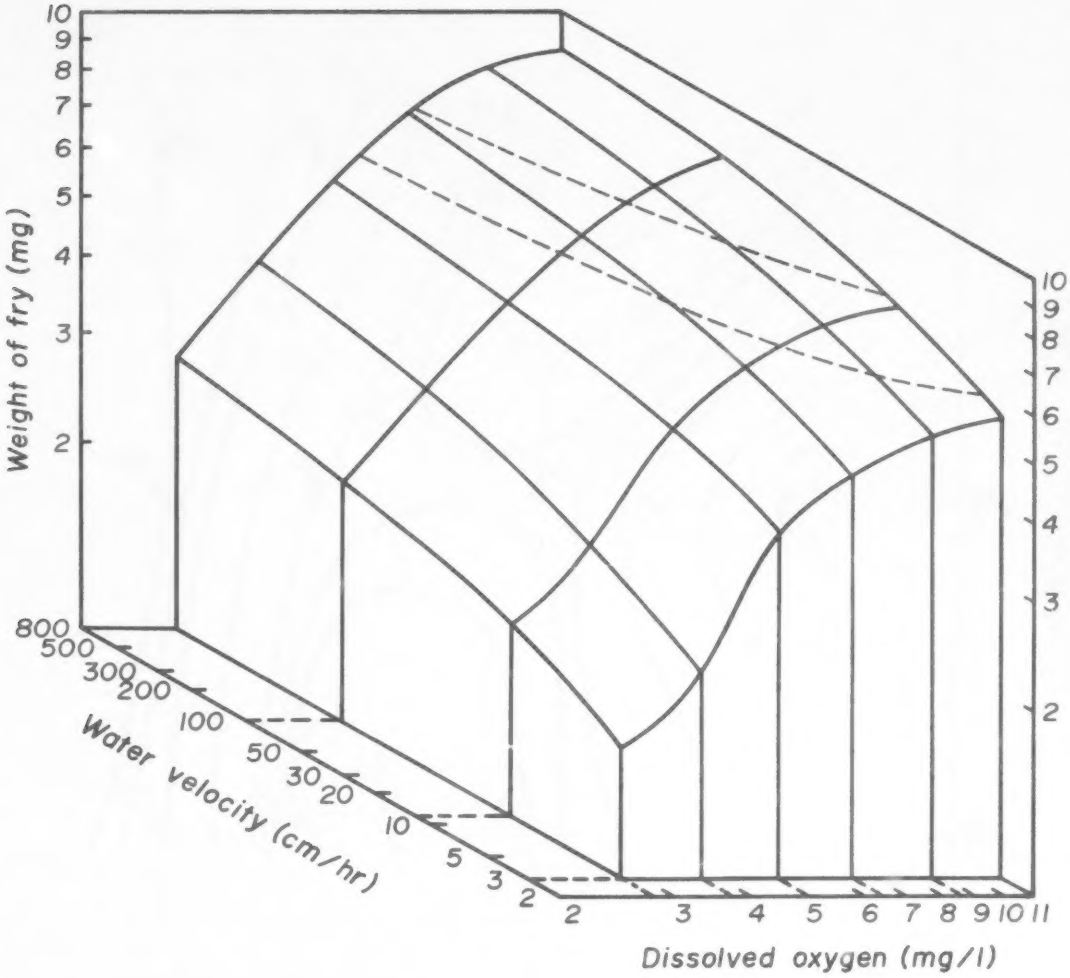

Figure 20. A three-dimensional diagram showing the influence of both oxygen concentration and water velocity on the mean dry weights of newly hatched coho salmon fry developing from embryos reared throughout development at the various combinations of oxygen concentration and water velocity represented by the intersection of the curves. After Shumway, Warren, and Doudoroff (1964).

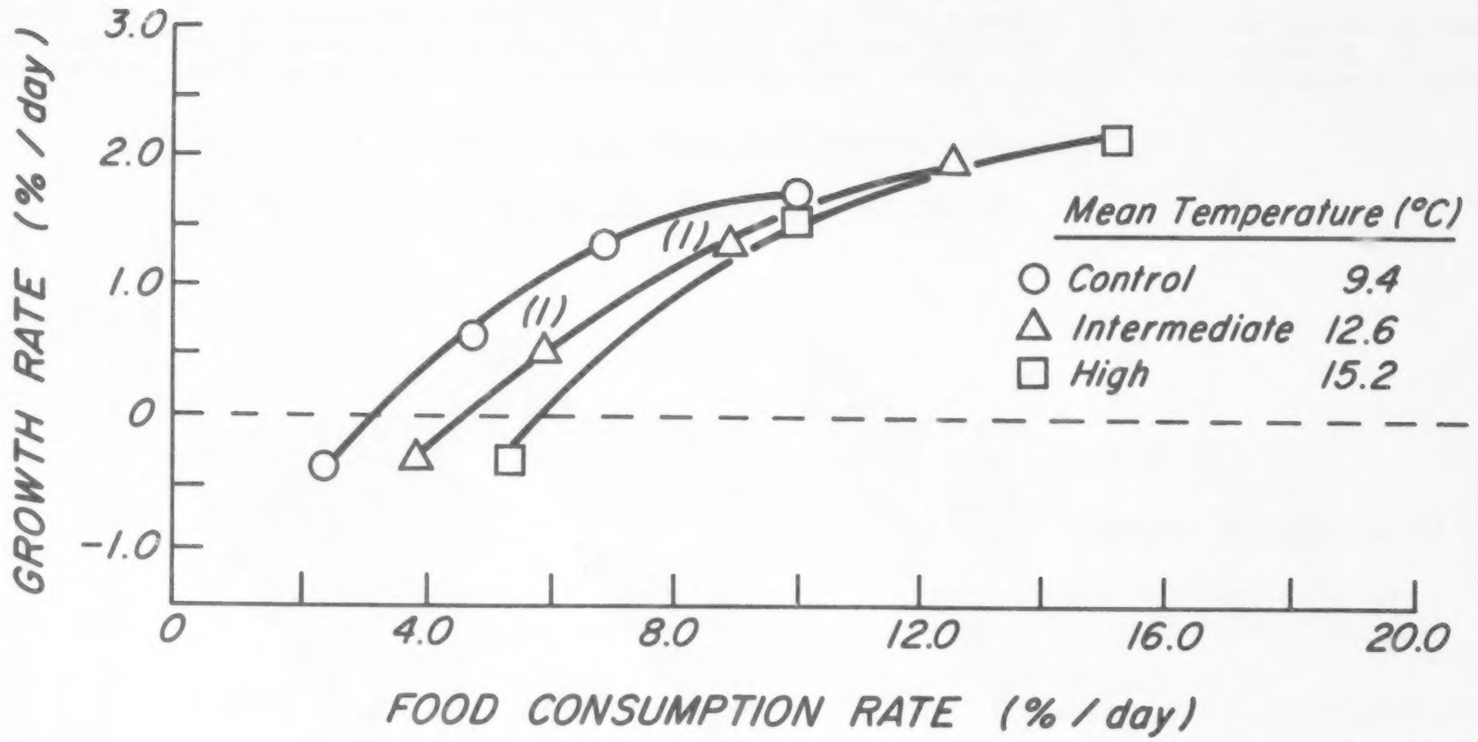

Figure 21. Relationships between mean rates of food consumption and growth of groups of steelhead trout kept at different fluctuating temperatures in spring experiment. Rates of food consumption and growth are expressed in dry weights. The initial mean wet weight of the fish was 2.29 g. Numbers in parentheses indicate the number of fish which died in a treatment. After Wurtsbaugh (1973).

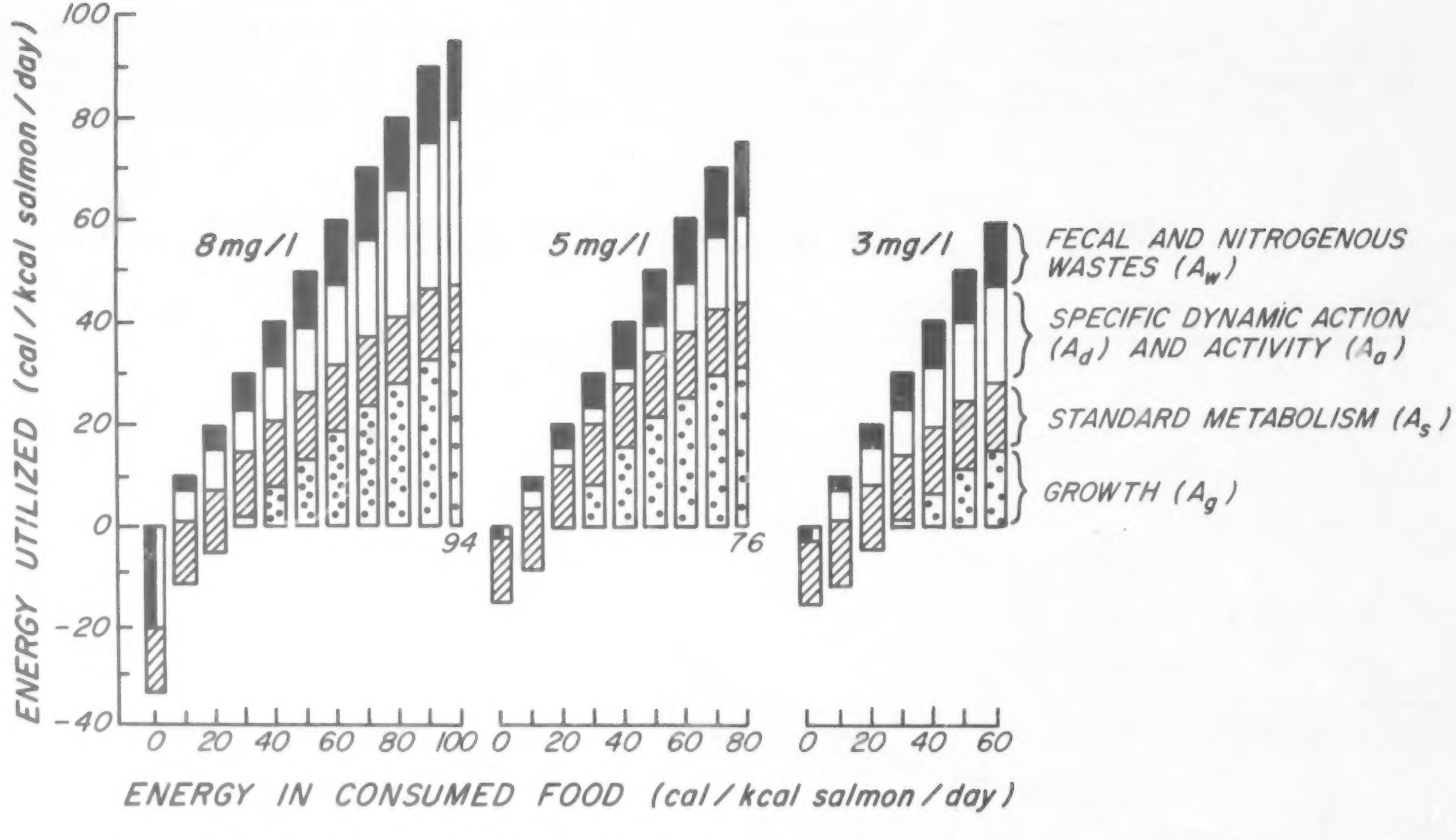

Figure 22. Energy budgets showing relationships between food consumption rate, energy and material uses and losses, and dissolved oxygen concentration for juvenile coho salmon in laboratory studies at 15C in the summer. The influence of both food availability and oxygen concentration on scope for growth are apparent in differences in growth parts of these budgets. After Thatcher (1975).

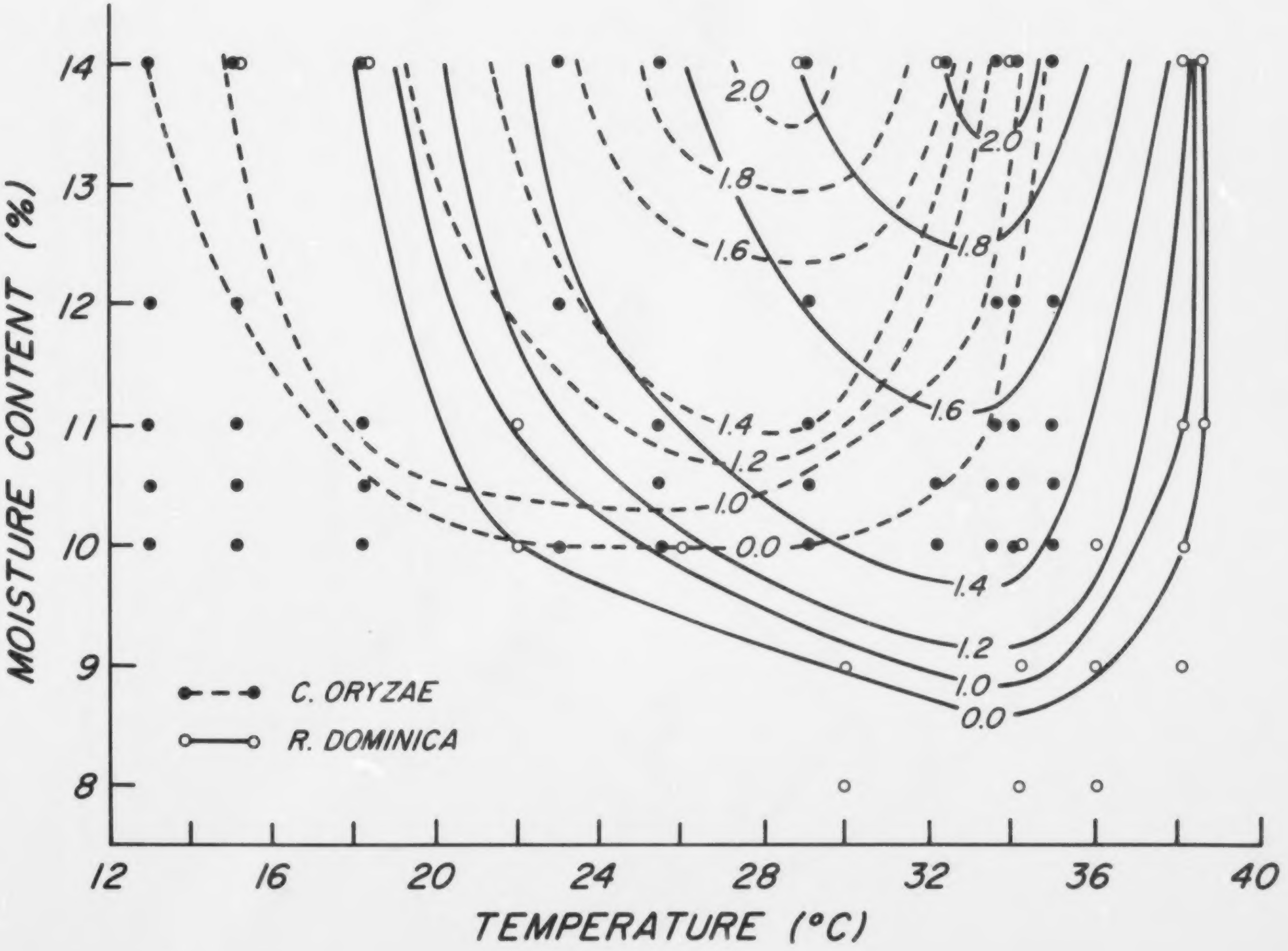

Figure 23. The finite rate of increase (λ) as a function of temperature and moisture for the grain beetles, *Calandra oryzae* and *Rhizopertha dominica* living in wheat. Rates of increase are indicated by contour lines that describe conditions with identical values of λ. After Andrewartha and Birch (1954).

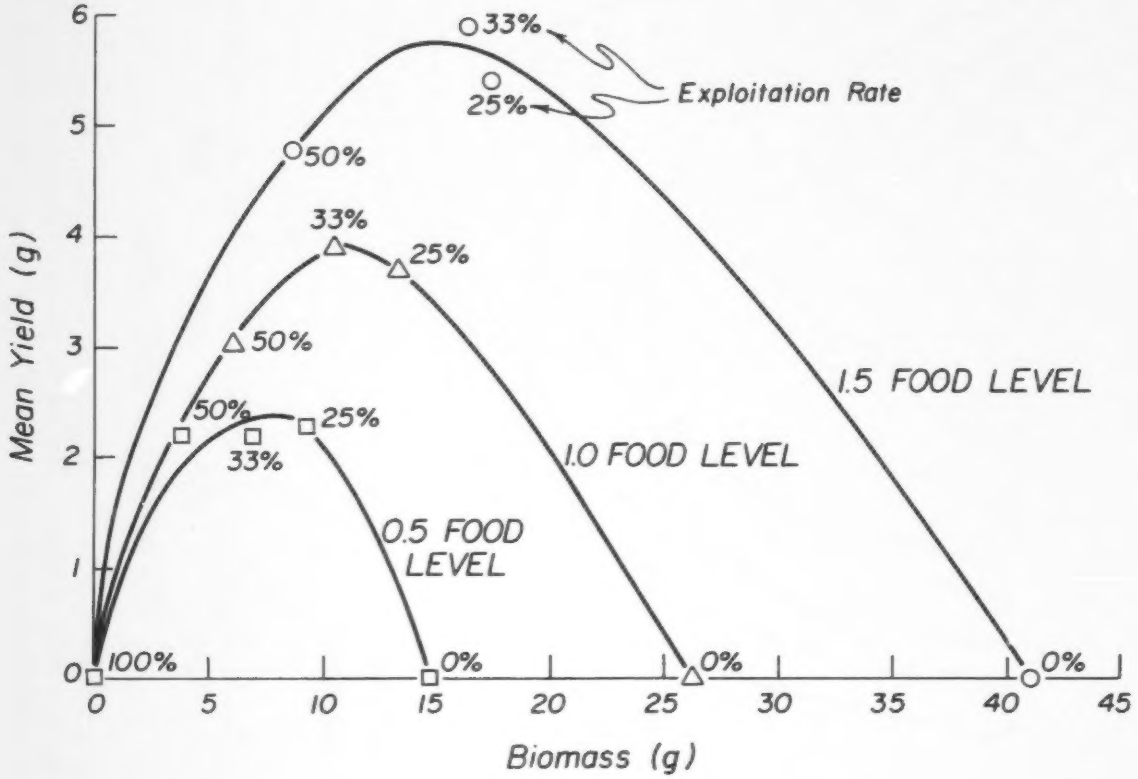

Figure 24. Curves indicating relation of yield of guppies per 3-week brood interval to biomass and exploitation rate (indicated percentages) at each diet level. Points indicated for 0 percent exploitation rate are average population levels for the 3 weeks immediately before exploitation. After Silliman (1968).

In Figure 25, we illustrate how different levels of productivity determine the magnitude of production curves for trout in laboratory stream systems. Production is defined as total tissue elaboration, and it can be determined as the product of mean relative growth rate and mean biomass. Different light levels and different current velocities led to different algal community structures, different levels of food (insects) availability, and so to different relative growth rate relationships with biomass, and thus to different production curves. Such systems of production curves entail not only differences in production performance under different conditions but also differences in the capacities of the laboratory stream systems to produce trout--the productivities of the streams for trout.

Toxicants can affect production rates by the direct effects they have on the growth of individuals in a population. Unstabilized effluents of the kraft pulp and paper process can, at some concentrations, directly affect the scope for growth performance of salmonids at different rates of food consumption (Fig. 26A). This can be shown to lower production curves for groups of salmonids, even when food availability in laboratory streams remains unaffected (Fig. 26 B). Seim et al. (1977) have summarized some of the research on this problem conducted at our laboratory. With other toxic substances, for example dieldrin introduced at very low concentrations, effects on the production of fish (Fig. 27B) appear to be mediated more by reduction in the availability of their food resources than by direct effects on food utilization for growth (Fig. 27A).

The dynamics of community structure--the changes in abundances of constituent populations--whether measured in laboratory or natural communities, demands the use of theories or models, if it is to be understood in terms of environmental factors and interactive individual organism and population performances. This is so not only for dynamic but also for steady-state community behavior. Even under constant environmental conditions, population densities and community structure are time variant until some possible steady state is reached (Fig. 12). But any steady state that may be reached is only one of an infinite number of possible such states (Fig. 12). And these, are determined by the levels of all environmental factors including any effective toxicants present (Figs. 6, 12). One reason we earlier described the population system of algae and protozoa developed by Taub (1973) was her synthesis of empirical laboratory research with simulation modeling. This permitted her to determine nutrient concentration, light inentsity, and exchange flow rate scopes for steady-state density structure, or performance, of the two-species system she studied (Fig. 13). The introduction of an effective toxicant would directly or indirectly affect the interacting populations (Fig. 12), and so alter their dynamic and steady-state behavior, their scopes for density performance, and scope for persistence of the two-population system.

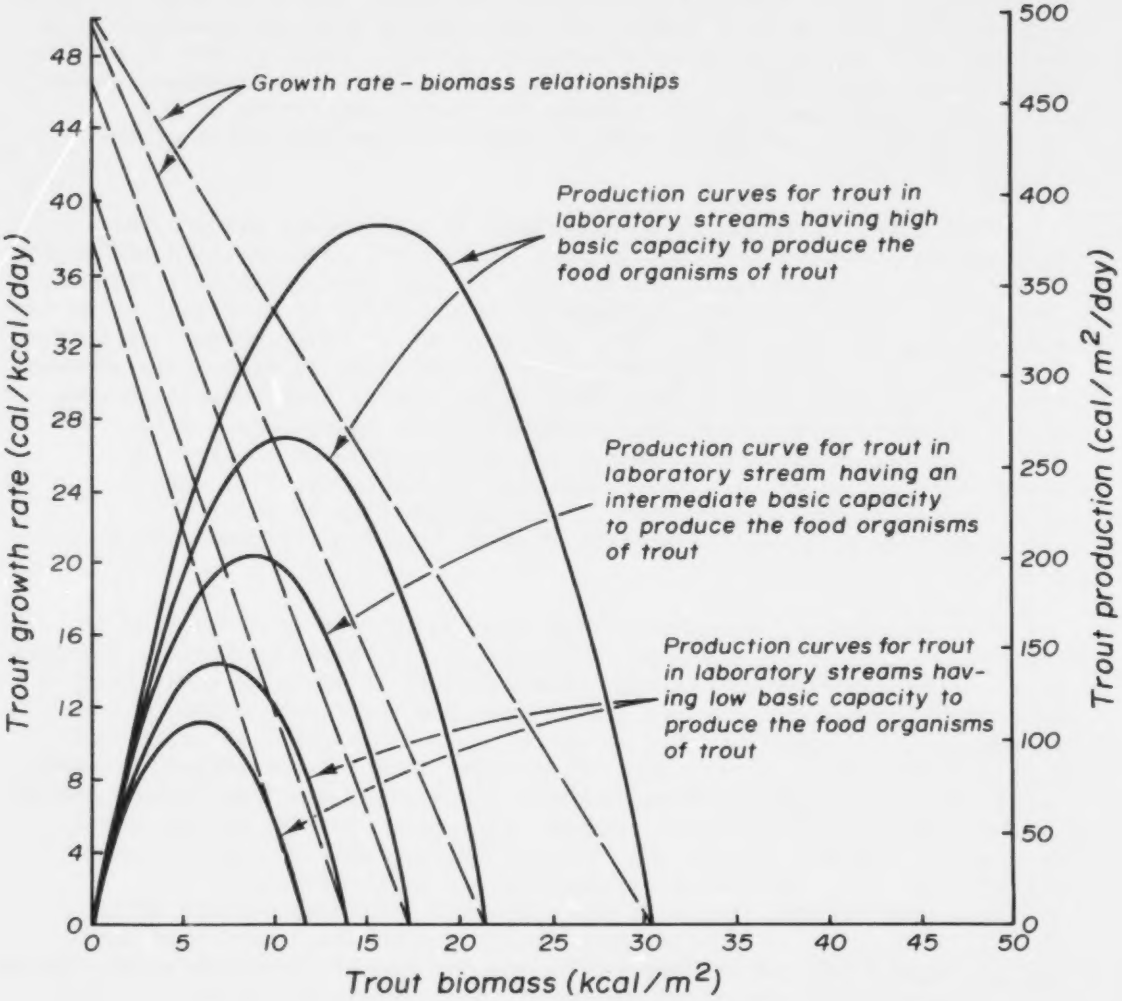

Figure 25. Approximations of biomass-production curves for cutthroat trout in the laboratory stream ecosystems having five different basic capacities to support trout production in the spring 1968 experiment. After Warren (1971).

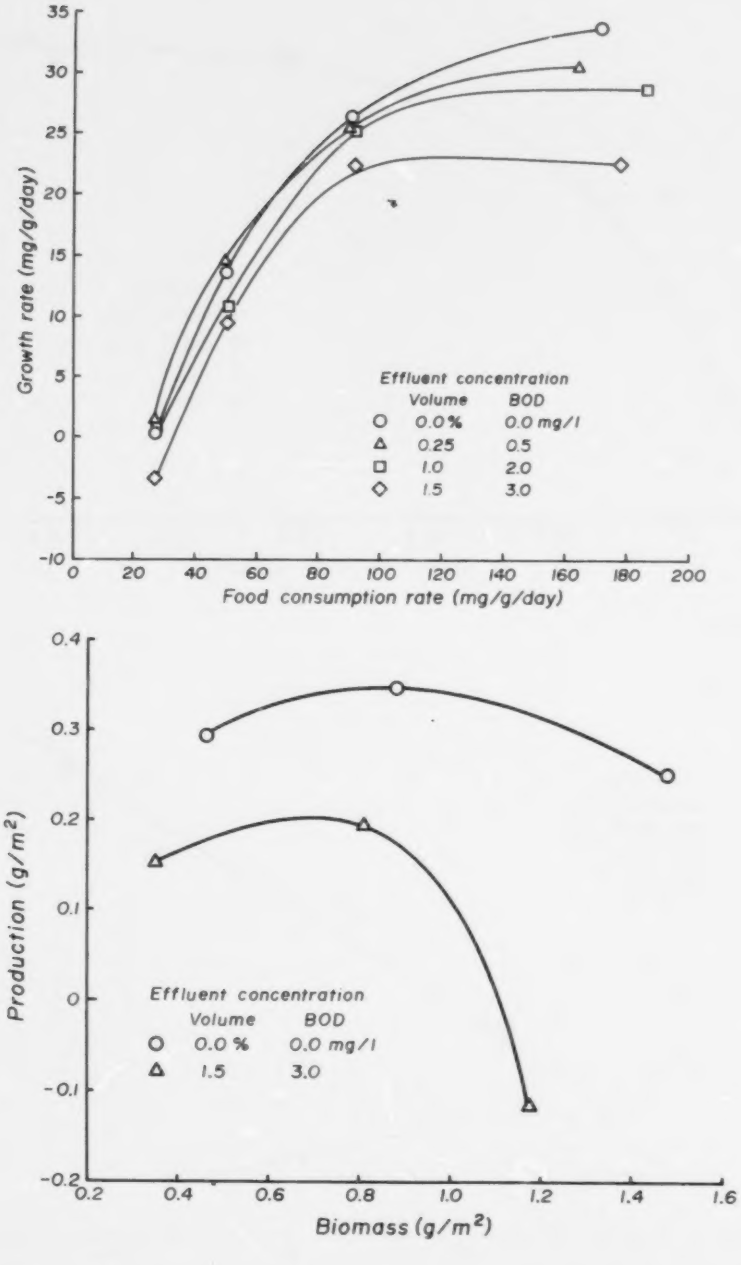

Figure 26. Relationships between food consumption and growth of juvenile chinook salmon at different concentrations of kraft process pulp and paper mill effluent, when the fish were fed controlled rations in aquaria (A). And (B) relationships between the biomass of juvenile chinook salmon and their production in laboratory streams receiving similar effluent and in streams not receiving such effluent. After Tokar (1968) and Seim et al. (1977).

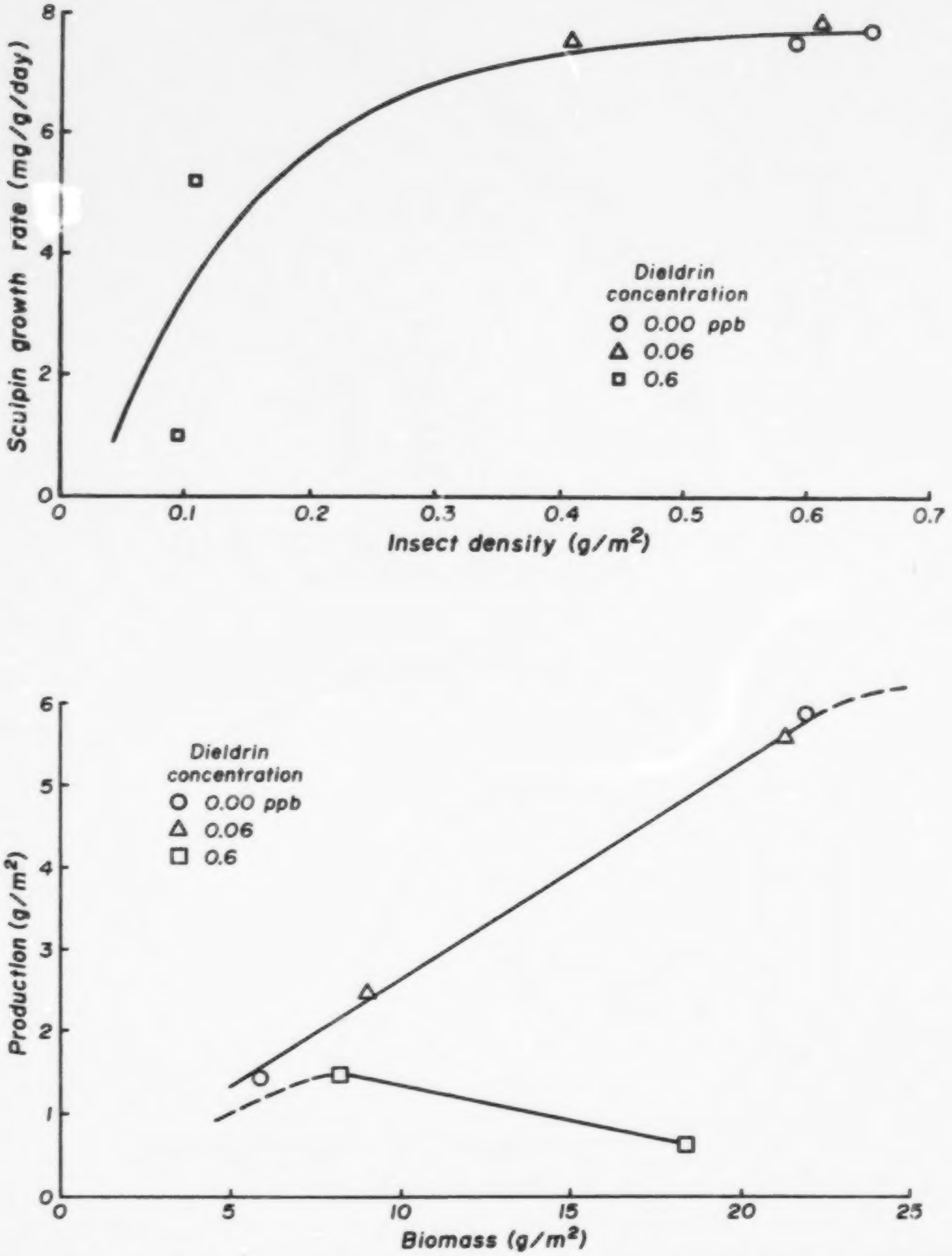

Figure 27. Relationships between the growth rate of sculpins and the density or biomass of the insects upon which they fed in laboratory streams into which different concentrations of dieldrin were introduced (A). And (B) relationships between the biomass of sculpins and their production in the same streams. After Warren (1971).

D. ON THE ADEQUACY OF EMPIRICAL INVESTIGATIONS IN ENVIRONMENTAL TOXICOLOGY

Before we finally move on to consider the entire matter of design, interpretation, generalization, and application of theoretical and empirical studies in environmental toxicology, let us briefly consider the general problem of the adequacy of empirical investigation. For the problem of empirical adequacy in environmental toxicology is the problem of empirical adequacy in biological investigation confounded by the introduction of innumerable toxic substances having practically unknown action and effect sequences. *Whatever is an empirical difficulty in biology must be a much greater empirical difficulty in environmental toxicology, and the addition of human social dimensions further aggravates this difficulty.*

Before considering criteria of empirical adequacy, we have first to consider the matter of *what it is that empirical work is to be adequate for:* What are its objectives, or the problems to be solved? For that part of environmental toxicology with which we have here been concerned, empirical investigations could have as their ultimate objectives: the screening of toxic materials for decisions as to their possible introduction into the environment; development of criteria for setting standards to protect various organisms, including man, and even biological communities; explanation and understanding of the behavior and effects of toxic substances in ecological systems for levels from the individual organism upward; and some combination of these. Some notion of prediction is generally involved in application of empirical results or in testing of explanations. But we, at least, are always uncomfortable about screening decisions and standards based on little explanation and understanding, although we do recognize the need for decisions and standards even when explanation and understanding may not be entirely adequate.

Yet some sort of rationale, based on some sort of understanding of a problem, must always be involved in human decisions. With regard to the empirical basis of any such understanding, we would be well advised to remember the raw data of experience are in no way an explanation, no matter how extensive the data may be. The data present a need for explanation: the data are the explanatory problem, not its solution. At most from data we can hope to get empirical generalizations by some sort of inductive process (Fig. 1). But many empirical generalizations are usually necessary to account for vast accumulations of data. And it is difficult to see the relationships among these generalizations and the boundary conditions for application of any one of them. Moreover, empirical generalizations often seem to be contradictory, even though they might not be, were we to understand more. *Regardless, the objective of empiricial work should be attainment of the most general and reliable empirical generalizations possible; not quantitative prediction, for which it is generally quite unsuited.*

But by what criteria are we to evaluate empirical studies in environmental toxicology? In an earlier section, we suggested that theories should, at least in part, be evaluated according to their dimensional, dynamic, and empirical adequacy. Perhaps laboratory models of biological systems should be evaluated on the basis of their *representational adequacy* and the *generality* of their results. In some sense, adequacy with regard to all *other pertinent empirical work*, with regard to *conceptual framework considerations*, and with regard to *theoretical considerations* must be involved. No empirical result can be evaluated outside a broader context of empirical experience, conceptual framework, and theory. Neither can it be applied to solution of problems in environmental toxicology without some conceptual framework or theory consciously or subconsciously being employed. It is for this reason that we emphasize that conceptual framework and theoretical adequacy as well as representational adequacy and generality ought to be employed as criteria for evaluation of empirical work in environmental toxicology.

By *representational adequacy*, we mean that, in dimensional and dynamic terms, a laboratory biological system should with some positive degree of reliability represent the classes of objects and relations of a natural system of interest. Both the organismic system and the environment involved in the biological system in the laboratory should satisfy this criterion. Because we have access to natural organismic systems for laboratory studies at the individual organism level, and because reasonably representational environments can often be developed for individual organisms, we believe representationally adequate laboratory studies of individual organisms are possible. At the population level, for small organisms with short life histories, some degree of representational adequacy may be achieved, although environmental considerations become more critical. But the problem of creating representationally adequate multispecies systems in the laboratory is much greater. For, at this level of organization, we are deeply involved in determining not only the environmental part of the system but the very nature of the organismic system itself: we in large part create the capacity of the multispecies system by bringing together individual species having different capacities of their own.

The criterion of *generality* of the results of laboratory biological system studies is exceedingly difficult to achieve, or at least to know that it has been achieved. And, yet, in some respects it is as important as the criterion of representational adequacy. For no matter how well we may have represented some particular biological system in nature, our results can be of only very limited scientific and practical value if they cannot be applied to other biological systems. This again raises the whole problem of empirical generalization: we can at most study only a relatively few biological systems, and yet our problems are with many; we must generalize, but with the limited possibilities of empirical experience, we cannot know the boundaries of applicability of empirical generalization. This is one of the most fundamental reasons for theory as a scientific deductive system through which empirical generalizations can be deduced, explained, and at least theoretically bounded. Adequate *schemes of classification* of organismic systems on all levels of biological organization are absolutely essential to deal with the problems of generality. This is as necessary for the conceptual and theoretical parts of our investigative endeavors as it is for their empirical parts. Only through the development of more adequate classification schemes at all levels of biological organization can we begin to deal with the problem of generality of the results of our investigations in environmental toxicology.

V. CONCEPTUAL, THEORETICAL, AND EMPIRICAL EFFORTS TO RESOLVE PROBLEMS IN ENVIRONMENTAL TOXICOLOGY

A. CONCEPTUAL AND THEORETICAL CONTEXTS OF PROBLEM PERCEPTION, DEFINITION, AND UNDERSTANDING

We must now return to the matter of evaluating the objectives of laboratory ecological system research in relation to problems in environmental toxicology. In earlier asserting this need, we acknowledged that such evaluation of objectives must be more subjective than the evaluation of methodological approaches in relation to objectives. But we have found that even the evaluation of methodologies is neither simple nor in itself objective: There can be valid differences of opinion as to the adequacy of particular methodological approaches to the achievement of the same objectives, for presumably such differences of opinion always have some rational basis for those holding them. Nevertheless, we cannot know the basis of these differences without at least some articulation of their presuppositions, either at the level of conceptual frameworks or at the level of theories. Without some specification of conceptual frameworks and theories, consideration of the adequacy of empirical approaches to objectives can hardly be rational.

Evaluation of objectives of research in relation to apparent problems is an even more difficult matter. This is so for several reasons. First, there can be valid disagreement as to the relevance of the objectives of particular scientific work to problems perceived and even defined in the same way. Second, problems associated with the same phenomena are not always perceived as being the same. And finally, problems in environmental toxicology are not simply scientific problems, perceived only by scientists and to be approached only with scientific objectives and methodologies. So, as with the evaluation of methodologies, the evaluation of the relevance of objectives to problems in environmental toxicology can be no simple and direct process, but rather one that must involve employment of conceptual frameworks and theories. But at this level of problem perception, definition, and understanding, conceptual frameworks and theories must involve that which is sociological as well as that which is more simply natural science.

For evidence of great differences in perception of problems associated with the same phenomena, we need look no further than the domain of phenomena and problems stimulating preparation of this article. Publication by Rachel Carson (1962) of her book *Silent Spring*, in which she articulated her view of the potential hazards of pesticides to man and his environment, stimulated a sometimes bitter controversy among scientists and laymen alike. The correctness or incorrectness of Miss Carson's view and whatever rational basis it may have had is not here at issue. What is at issue is that apparently deeply held beliefs of biochemists and ecologists and of agriculturalists and environmentalists led to such different perceptions of whatever problem or problems may have existed that the controversy over this book became extremely bitter. Neither is the correctness of the many very different perceptions of this problem that arose at issue here. Such differences in views may not in themselves be undesirable; indeed, they may be desirable, for no single view of complex phenomena and problems is likely to provide for understanding and problem solution. But without articulation of the different conceptual frameworks from which contrary perceptions of the problem arose and with no relevant theory, consideration of differences in problem perception and of what the total problem might really be like could not be rational: indeed, it became very irrational on all sides. Remnants of this controversy persist to this very day, biochemists, ecologists, agriculturalists, foresters, and environmentalists continuing to disagree in the absence of adequate conceptual frameworks and theories. And because toxic substances in the environment present a social problem of vast complexity and of potential as well as actual importance, the sort of problem science as presently pursued cannot handle, it has been left to legislative, judicial, and administrative bodies for resolution, still with inadequate scientific understanding available.

Thus it would seem, in the whole domain of environmental toxicology, we have not only to conceive of and employ conceptual frameworks and theories in the evaluation of objectives in relation to problems, we have also to employ these in attempting to perceive and define just what the problems may be. But these could be no ordinary conceptual frameworks and theories, for they would need to subsume that which is social and technological as well as that which is more nearly the domain of the natural sciences. Less than this is apt to ever leave problem perception, definition, and solution short of being rational. With realization of our ever too limited social and scientific capacities, even vague perception of such a need may cause us to back away and do other things now easily rationalized but probably ever too partial to solve our problems. And yet, surely the continued need to employ toxic substances--pesticidal, medicinal, and other--and the continued potential hazard of these is of such vast importance to man that he will expend great resources and efforts in problem evaluation. Some of these resources and efforts ought to be expended in approaching that which may seem unapproachable but which, so long as the possibility of some success exists, cannot justly be avoided. Such frameworks deserve and need to be articulated to provide greater rationality in human social and scientific endeavors. That the domain of environmental toxicology is vast and may never be subsumed with full adequacy in no way lessens the need for us to begin to approach the development of conceptual frameworks and theories sufficiently universal for adequate problem perception, definition, and understanding.

In the recorded history of man, so often his ideas and other creations have not accomplished that for which they were intended and have led to social problems, we cannot help but wonder what creations ought to be encouraged and what might best be avoided. But it would not be desirable, and certainly would not in the long run be possible, to place any controls whatsoever on human imagination and the search for understanding and better world systems for man. We do not believe that understanding or the ideas for concrete creations can be shown to be responsible for social problems but rather that problems are owing always to insufficient understanding and the uses to which ideas are put. In this, our harmful experiences with toxic substances are no exception. If there had been or could be something like adequate understanding of social and natural systems in all their interrelationships, *and were individuals and societies to behave more rationally*, these and other human experiences could have been quite different, much more beneficial and much less harmful. But in the absence of universally articulated understanding of social-natural systems, their capacities and possible behaviors under all possible abstractly conceivable conditions, we have no reason to suppose but that too many human experiences will continue to be harmful. It is not the idea or invention of a terribly persistent and toxic substance but rather the decision to develop and employ it widely that can lead to economic and social dependencies, very harmful side effects, and later attempts to correct apparent errors, these attempts then leading to further social problems. If there could be a general theory of management of toxic substances, which would universally articulate understanding of natural and social systems, there might be some hope that the long sequence of human errors could in the future be more often interrupted. But it seems almost impossible to conceive of what such a theory might be like--what its form and content would be.

The problem of management of toxic substances is not unlike the problem of management of natural resources. Even were we to have a very universal theory of, say, fisheries or forest exploitation--which we do not--we would yet not have a theory of management of these resources. A universal theory of fisheries or forest exploitation could tell us the yields obtained at different rates of exploitation under various physical and biological conditions and what other ecosystem effects would occur. But it would not tell us what a society might choose to do with these resources or want of these ecosystems under various circumstances determining the behavior of that society. Failures of present day fisheries and forest management to account adequately for societal demands have led to entry by legislative and judicial bodies into the business of resource management, usually to the chagrin of the professionals. Because toxic substances have been employed widely in attempts to manage renewable resources and have thus led to some of our most prevalent problems, it is not inappropriate, for the moment, to consider these management problems together. Indeed, a theory for one would need to entail a theory for the other, in many applications of the theory.

In some sense, such a theory would need to subsume all the biological and physical effects of different kinds and levels of use and all possible societal behaviors leading to or influenced by these possible uses. Only in this way could the many possible interrelated action and effect webs be explained, understood, and anticipated to the extent necessary to avoid resource, toxic substance, and social problems. We are thinking here of theory as a scientific deductive system, articulated in abstract language, interpretable in observational language as necessary, and universal in the sense of being invariant and general. We recognize that most if not all our colleagues in the natural sciences and friends in the social sciences will say no such theory is possible, certainly not now, probably not ever. And they are probably correct. But somehow the question keeps returning to haunt us: Can we afford to avoid the attempt?

Any such attempt, it seems to us, should begin not at the conceptual level of formal theory but rather at the level of what we have been calling conceptual frameworks. The rush to formality, in our opinion, has too often in biology and the social sciences led to excessively partial views that can only be externally inadequate, whatever the merits of the achieved internal consistency.

Theories arise out of implicit or explicit conceptual frameworks, which give theories much of their meaning. And at this stage it is not the language or the form of theory that must concern us. Rather, we must first achieve some outermost abstract description of what the domain of concern, here social-natural systems, might be like. This is what Warren, Allen, and Haefner (MS) attempted to do for biology with the set of four generalizations presented very early in this article. Such an abstract verbal description, with the aid of its rules, should tell us something of what a theory or theories would need to do to articulate adequately that which lies behind, determines, and so could explain phenomena in the domain of concern. Only then can we rationally approach the matter of language and form of theories to be articulated.

Communication with full understanding even within broad disciplines is difficult. Between different disciplines, say the physical, the biological, and the social sciences, it is not at all apparent that communication occurs sufficiently well for the integrated thought and understanding necessary to achieve unified theory. Among the most important reasons for making conceptual frameworks explicit is that, even when different views are held, rational discussion based on the frameworks can proceed, for the basis of arguments and judgments can be examined by all. And it is possible that a universally adequate conceptual framework for biology, differently interpreted, would be found to be in some degree adequate for the social sciences. If it were found not to be so, it might, for the same underlying reasons, not be so adequate as it was believed to be for biology. In any event, it is quite possible that some conceptual framework could be developed that would subsume the biological and social sciences. And, it is our belief, that even before adequate theoretical languages and forms could be found and employed in the articulation of any sort of general theory of management of toxic substances, the conceptual framework itself would be found to be useful in the resolution of some problems. Indeed, the process of developing a framework, however successful the product, would be beneficial in bringing the different disciplines together, for many of our problems appear to have their roots in our failure to do this.

In the absence of articulated conceptual frameworks and theories adequate to subsume that which is social as well as that which is more directly physical and biological, we cannot rationalize problem perception, problem definition, the relevance of objectives to problem solution, and approaches to these objectives in environmental toxicology. But anyone thinking for awhile about the whole domain of environmental toxicology can delineate what appear to be problems, possible social and scientific objectives perhaps relevant to the solution of these problems, and approaches to these objectives. That this can be done is in itself evidence of some *a priori* conceptual basis for any such effort and delineation. Nevertheless, without articulation of this conceptual basis, either as a framework or a theory, we cannot demonstrate whatever rationality our delineation may have; although, in view of rather obvious human social problems, the effort at least would appear to be pragmatically rational. In any case, we can here not proceed without some delineation of social problems and institutional objectives and approaches--as we have attempted to do in Figures 28 and 29--before we proceed to evaluate the relevance of objectives of laboratory ecosystem research in environmental toxicology.

In delineating problems, objectives, and approaches in environmental toxicology, we ought to begin with some theoretical notion of the relations of societies to their total environments. Such a notion, however, would be exceedingly difficult to articulate, because man's ideas become part of the environment of particular societies and influence their behaviors as wholes: To think of the environment of a society only in mere physical terms is to leave out much that would be necessary to understanding of its behavior. Now all organismic systems, at whatever levels of organization, behave as though they have goals. However we may account for such behavior in nonhuman organismic systems, man certainly perceives goals, and the ways in which these are perceived have much to do with the behaviors of human social systems. Goals and the possibilities of achieving them are determined by geographic, cultural, political, technological, and scientific heritages and states, as we suggest in Figure 28. Social problems are perceived in the creation and utilization of human environments intended to satisfy needs and aspirations--problems that perhaps can generally be categorized as being resource, cultural, political, or technological (Fig. 28). With the intent to resolve these problems, implicit and explicit objectives are imperfectly perceived and articulated, and institutional approaches to these problems and objectives are conceived. But these objectives are not always externally consistent and their pursuit may aggravate and create problems as well as lead to some solutions (Fig. 28). And the methods of human institutions may or may not, singly or together, be adequate for realization of objectives.

We may think of the institutional approaches to social problems as being legislative, judicial, administrative, educational, technological, and scientific (Fig. 28). Here we are most directly concerned with scientific approaches, and Figure 29 is our cursory attempt to delineate something of the goals, problems, objectives, and methods of the scientific institution. But, so long as our ultimate concern is with social goals, problems, and objectives, as it must be in environmental toxicology, our scientific institution must be seen to contribute to social achievement in the context of all human institutions. We can take the ultimate goal of man's scientific institution to be the continuous advance of human understanding (Fig. 29). Such understanding as is achieved may be used in the resolution of social problems.

Understanding is advanced by theoretical and empirical explanations within the context of existing conceptual frameworks. And scientific

HUMAN ENVIRONMENT

⇕

MAN

SOCIETAL, GROUP, AND INDIVIDUAL

GOALS - POSSIBILITIES

ACCORDING TO GEOGRAPHIC, CULTURAL, POLITICAL
TECHNOLOGICAL, AND SCIENTIFIC HERITAGES AND STATES

SOCIAL PROBLEMS ARE PERCEIVED
IN THE CREATION AND UTILIZATION OF HUMAN ENVIRONMENTS
INTENDED TO SATISFY NEEDS AND ASPIRATIONS

RESOURCE PROBLEMS   CULTURAL PROBLEMS   POLITICAL PROBLEMS   TECHNOLOGICAL PROBLEMS

IMPLICIT AND EXPLICIT OBJECTIVES FOR RESOLUTION OF SOCIAL PROBLEMS
IMPERFECTLY PERCEIVED AND ARTICULATED

INSTITUTIONAL APPROACHES TO SOCIAL PROBLEMS ARE CONCEIVED
LEGISLATIVE   JUDICIAL   ADMINISTRATIVE   EDUCATIONAL   TECHNOLOGICAL   SCIENTIFIC

OBJECTIVES OF INSTITUTIONAL APPROACHES
INTENDED TO RESOLVE SOCIAL PROBLEMS
BUT NOT ALWAYS CONSISTENT AND THEIR PURSUIT
MAY AGGRAVATE AND CREATE PROBLEMS

METHODS OF HUMAN INSTITUTIONS
MAY OR MAY NOT, SINGLY OR TOGETHER,
BE ADEQUATE FOR REALIZATION OF OBJECTIVES

objectives and methods of scientific, technological, educational, and governmental institutions generally involve redefinition of social problems in ways making institutional approach possible, but such redefinition often makes approaches ineffective or irrelevant

Figure 28. Delineation of human goals, problems, institutions, and institutional objectives and approaches.

HUMAN ENVIRONMENT

⇕

MAN'S SCIENTIFIC INSTITUTION

GOAL

THE CONTINUOUS ADVANCE OF HUMAN UNDERSTANDING

SUCH UNDERSTANDING AS IS ACHIEVED MAY BE
USED IN THE RESOLUTION OF SOCIAL PROBLEMS
BUT MAY ALSO CREATE NEW SOCIAL PROBLEMS

UNDERSTANDING IS ADVANCED BY

THEORETICAL AND EMPIRICAL EXPLANATIONS WITHIN

THE CONTEXT OF EXISTING CONCEPTUAL FRAMEWORKS

PERCEPTION AND DEFINITION OF SCIENTIFIC PROBLEMS

THEORETICALLY OR EMPIRICALLY

PROBLEMS THAT ARE FIRST PERCEIVED AS
BEING SOCIAL AND GENERALLY REDEFINED SO
AS TO MAKE SCIENTIFIC APPROACH POSSIBLE,
BUT IN SO DOING, APPROACH MAY BE MADE
INEFFECTIVE OR IRRELEVANT

SCIENTIFIC OBJECTIVES

PRESUMED TO BE RELEVANT TO
SOLUTION OF DEFINED PROBLEMS

SCIENTIFIC METHODS

PRESUMED TO BE ADEQUATE
FOR REALIZATION OF OBJECTIVES

THEORIES	MODELS	OBSERVATIONS
PROBLEM PERCEPTION AND DEFINITION - FORMALLY EXPLAIN OR GIVE MEANING TO OBSERVATION AND EXPERIENCE - THEMSELVES GIVEN MEANING NOT ONLY BY OBSERVATIONAL VALIDATION BUT ALSO BY PREVAILING CONCEPTUAL FRAMEWORK		PROBLEM PERCEPTION AND DEFINITION - MUST BE EXPLAINED OR GIVEN MEANING BY CONCEPTUAL CONSTRUCTS

Figure 29. Delineation of the goals, problems, objectives, and approaches of man's scientific institution.

problems are defined, either theoretically or empirically, within the same contexts. In this process, we would note that problems which are first perceived and defined in social terms are generally redefined so as to make the scientific approach possible. But such redefinition, as necessary as it may be in the pursuit of science, often makes the scientific effort ineffective or even irrelevant to possible solution of the problems originally motivating the effort. We are reminded that Kenneth Boulding once observed science to be the process of substituting unimportant problems we can solve for important ones we cannot.

B. APPARENT AND POSSIBLE OBJECTIVES OF LABORATORY ECOLOGICAL SYSTEM STUDIES

We have prepared Figure 30, as much for ourselves as for others, to help keep the objectives of laboratory ecological system studies in the context of all scientific problems, other biological problems, and other approaches in environmental toxicology. As important as may be the possible objectives and results of laboratory ecological system studies, they directly relate to only a part of the scientific problem, let alone technological, governmental, and educational problems, in environmental toxicology. And the possible contribution of such laboratory system research is better seen in relation to the whole.

In defining apparent and possible objectives of laboratory ecological system studies in environmental toxicology, we have attempted to be clear in distinguishing among them and to be reasonably comprehensive, without excessive proliferation. Of course, decompositions into subobjectives of the major objectives that we do present is desirable and is done in practice. Although we have already given examples from the literature of work that appears to have been directed toward these objectives, we will make no attempt here to classify this work according to objectives. Any such classification, we believe, will be evident enough.

In Figure 31 we list, in the first line, our view of the major apparent and possible objectives of laboratory ecological system studies in environmental toxicology: assay of the relative toxicity of substances; determination of the behavior of toxic substances; determination of the effects of toxic substances on individual organisms; determination of the effects of toxic substances on biological populations; and determination of the effects of toxic substances on biological communities. To be more general, these objectives should probably have included the notion of *cause* as well as *effect*. For, certainly, it may reasonably be argued that one of the reasons for laboratory studies is to make possible causal or operational explanation of phenomena we perceive in nature. But causal relationships cannot be observed, as we earlier emphasized. And so far as ecological explanation is involved, adequate observation of effects on performances at individual, population, and community levels of biological organization can be articulated into operational or causal explanations, but only with dimensionally, dynamically, and empirically adequate conceptual structures that are causal-deterministic.

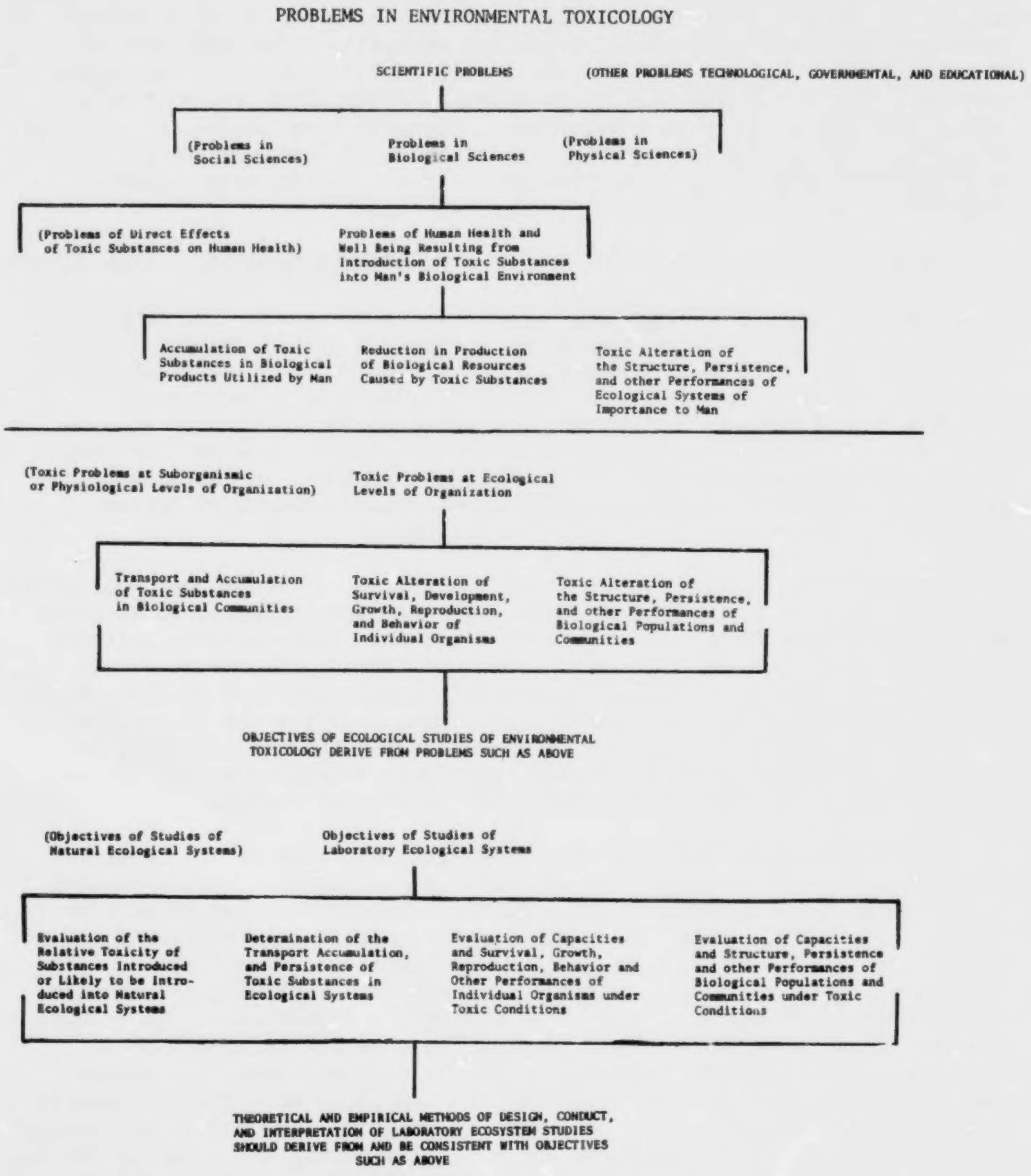
PROBLEMS IN ENVIRONMENTAL TOXICOLOGY
SCIENTIFIC PROBLEMS
(OTHER PROBLEMS TECHNOLOGICAL, GOVERNMENTAL, AND EDUCATIONAL)
(Problems in Social Sciences)
Problems in Biological Sciences
(Problems in Physical Sciences)
(Problems of Direct Effects of Toxic Substances on Human Health)
Problems of Human Health and Well Being Resulting from Introduction of Toxic Substances into Man's Biological Environment
Accumulation of Toxic Substances in Biological Products Utilized by Man
Reduction in Production of Biological Resources Caused by Toxic Substances
Toxic Alteration of the Structure, Persistence, and other Performances of Ecological Systems of Importance to Man
(Toxic Problems at Suborganismic or Physiological Levels of Organization)
Toxic Problems at Ecological Levels of Organization
Transport and Accumulation of Toxic Substances in Biological Communities
Toxic Alteration of Survival, Development, Growth, Reproduction, and Behavior of Individual Organisms
Toxic Alteration of the Structure, Persistence, and other Performances of Biological Populations and Communities
OBJECTIVES OF ECOLOGICAL STUDIES OF ENVIRONMENTAL TOXICOLOGY DERIVE FROM PROBLEMS SUCH AS ABOVE
(Objectives of Studies of Natural Ecological Systems)
Objectives of Studies of Laboratory Ecological Systems
Evaluation of the Relative Toxicity of Substances Introduced or Likely to be Introduced into Natural Ecological Systems
Determination of the Transport Accumulation, and Persistence of Toxic Substances in Ecological Systems
Evaluation of Capacities and Survival, Growth, Reproduction, Behavior and Other Performances of Individual Organisms under Toxic Conditions
Evaluation of Capacities and Structure, Persistence and other Performances of Biological Populations and Communities under Toxic Conditions
THEORETICAL AND EMPIRICAL METHODS OF DESIGN, CONDUCT, AND INTERPRETATION OF LABORATORY ECOSYSTEM STUDIES SHOULD DERIVE FROM AND BE CONSISTENT WITH OBJECTIVES SUCH AS ABOVE

Figure 30. Problems, objectives, and methods of laboratory ecosystem studies in relation to those of other studies.

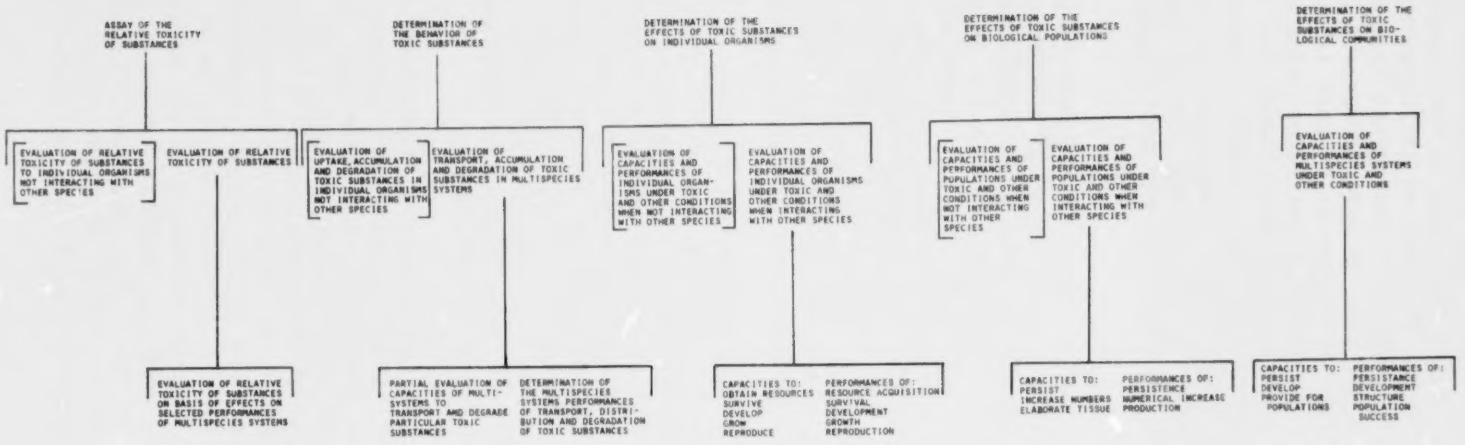
ASSAY OF THE RELATIVE TOXICITY OF SUBSTANCES
EVALUATION OF RELATIVE TOXICITY OF SUBSTANCES TO INDIVIDUAL ORGANISMS NOT INTERACTING WITH OTHER SPECIES
EVALUATION OF RELATIVE TOXICITY OF SUBSTANCES
EVALUATION OF RELATIVE TOXICITY OF SUBSTANCES ON BASIS OF EFFECTS ON SELECTED PERFORMANCES OF MULTISPECIES SYSTEMS
DETERMINATION OF THE BEHAVIOR OF TOXIC SUBSTANCES
EVALUATION OF UPTAKE, ACCUMULATION AND DEGRADATION OF TOXIC SUBSTANCES IN INDIVIDUAL ORGANISMS NOT INTERACTING WITH OTHER SPECIES
EVALUATION OF TRANSPORT, ACCUMULATION AND DEGRADATION OF TOXIC SUBSTANCES IN MULTISPECIES SYSTEMS
PARTIAL EVALUATION OF CAPACITIES OF MULTI-SYSTEMS TO TRANSPORT AND DEGRADE PARTICULAR TOXIC SUBSTANCES
DETERMINATION OF THE MULTISPECIES SYSTEMS PERFORMANCES OF TRANSPORT, DISTRIBUTION AND DEGRADATION OF TOXIC SUBSTANCES
DETERMINATION OF THE EFFECTS OF TOXIC SUBSTANCES ON INDIVIDUAL ORGANISMS
EVALUATION OF CAPACITIES AND PERFORMANCES OF INDIVIDUAL ORGANISMS UNDER TOXIC AND OTHER CONDITIONS WHEN NOT INTERACTING WITH OTHER SPECIES
EVALUATION OF CAPACITIES AND PERFORMANCES OF INDIVIDUAL ORGANISMS UNDER TOXIC AND OTHER CONDITIONS WHEN INTERACTING WITH OTHER SPECIES
CAPACITIES TO: OBTAIN RESOURCES SURVIVE DEVELOP GROW REPRODUCE
PERFORMANCES OF: RESOURCE ACQUISITION SURVIVAL DEVELOPMENT GROWTH REPRODUCTION
DETERMINATION OF THE EFFECTS OF TOXIC SUBSTANCES ON BIOLOGICAL POPULATIONS
EVALUATION OF CAPACITIES AND PERFORMANCES OF POPULATIONS UNDER TOXIC AND OTHER CONDITIONS WHEN NOT INTERACTING WITH OTHER SPECIES
EVALUATION OF CAPACITIES AND PERFORMANCES OF POPULATIONS UNDER TOXIC AND OTHER CONDITIONS WHEN INTERACTING WITH OTHER SPECIES
CAPACITIES TO: PERSIST INCREASE NUMBERS ELABORATE TISSUE
PERFORMANCES OF: PERSISTENCE NUMERICAL INCREASE PRODUCTION
DETERMINATION OF THE EFFECTS OF TOXIC SUBSTANCES ON BIOLOGICAL COMMUNITIES
EVALUATION OF CAPACITIES AND PERFORMANCES OF MULTISPECIES SYSTEMS UNDER TOXIC AND OTHER CONDITIONS
CAPACITIES TO: PERSIST DEVELOP PROVIDE FOR POPULATIONS
PERFORMANCES OF: PERSISTANCE DEVELOPMENT STRUCTURE POPULATION SUCCESS

Figure 31. Apparent and possible objectives of laboratory ecosystem studies in environmental toxicology.

Major objectives, such as the five we have just mentioned (Fig. 31), can be approached methodologically in the field and in the laboratory, as well as theoretically, in various ways. But here we are concerned most immediately with laboratory studies, especially ecological system studies in environmental toxicology. One point that we have endeavored to make clear in the second line of objectives in Figure 31 is that laboratory studies of individual organisms and populations not interacting with other species, that is, not parts of laboratory ecosystems, are an important way of approaching the relevant major objectives. Indeed, they may be a much better way than poorly designed laboratory ecosystem. We have, for this reason, shown enclosed in brackets in the second line of Figure 31 subobjectives for studies of individual organisms and populations not interacting with other species.

Achievement of the objectives *not enclosed in brackets* in the second line of Figure 31 would require investigation of multispecies systems or, at the individual and population levels, at least the presence of other species. The first of these objectives, evaluation of the relative toxicity of substances in multispecies systems, relates essentially to the employment of a complex organismic system as a reagent for assay of the toxicity of materials, much as individual organisms are employed in *bioassays*. The second objective in the second line of Figure 31 is determination of transport, distribution, and degradation of toxic substance in multispecies systems. This appears to be the objective of most of the recent laboratory ecosystem studies in environmental toxicology.

The three remaining objectives not enclosed in brackets in the second line of Figure 31 relate to determination of the effects of toxic substances on individual organisms, populations, and multispecies systems. And, in these objectives, we make what is probably *the most important distinction of all, the distinction between the capacities and the performances of organismic systems*. This distinction has rarely been made in either theoretical or empirical biological studies. And, yet, without it there is no way that we can conceive for achieving the sorts of universal explanations necessary for adequate solution of biological problems, including those in environmental toxicology.

Capacity of an organismic system, as we earlier explained, is a *theoretical concept* necessary to explain all possible performances of an organismic system in all possible environments. But if we must know something of the capacities, not just the performances, of organismic systems to be able to deal adequately with problems in environmental toxicology, and if capacity is a theoretical concept not empirically determinable, how are we to proceed? We cannot directly and fully evaluate theoretical concepts such as capacity, but indirectly and partially we can do so, or they would be of no value to us. We can measure particular kinds of performances of an organismic system under a wide range of combinations of environmental conditions of interest, in the laboratory. Under each set of conditions, the organismic system is likely to have a different level of any given kind of performance. We can thus determine the effects of environmental conditions on the *scope for performance* of the organismic system of interest, as we illustrated in Figures 13, 16, 17, 19, 20, 23, 25, 26, and 27. But scope for performance is yet an empirical concept: it is only a partial and indirect evaluation of the capacity of the system. For were the organismic system of interest to have been tested under other sets of environmental conditions, still other scopes for performance could have been determined all within the capacity of this system, all likely to be of some natural importance, and thus all of at least theoretical interest in the solution of problems of environmental toxicology. And were our organismic system of interest--individual organism, population, or multispecies system--to have developed under different conditions, its scope for performance under even the same subsequent conditions would very likely have been different. From some potential capacity, the realized capacity an organismic system develops will depend on environmental conditions during system development (Fig. 3). Developmental effects of toxicants on the capacities of organismic systems at all levels of biological organization should be of great concern. We can never fully or directly know these, but we must get as near to knowing them theoretically and empirically as we possibly can. Fundamentally, these are the reasons that we judge the distinction between capacity and performance, which we employ in articulating the objectives given in Figure 31, to be most important.

Thus the last three objectives that are not bracketed in the second line of Figure 31 relate to evaluation of effects of toxic substances on the capacities as well as on the performances of individual organisms and populations in multispecies systems and on the capacities and performances of multispecies systems as wholes. In the third line of Figure 31, we list some possible capacities and performances for each of these levels of biological organization. Individual organisms have capacities to utilize resources, survive, develop, grow, and reproduce. Evidences of these are the performances: resource acquisition, survival, development, growth, and reproduction, which we can measure. Similarly, population and multispecies systems have some capacity to persist, which we can partially evaluate by measurements of persistence, a performance. And, of course, there are other capacities and performances, at all levels of biological organization. In relation to the objective to determine transport, distribution, and degradation of toxic substances in multispecies systems, we should perhaps make one additional comment. Such behavior is, of course, determined in part by the physical-chemical nature of the toxicant, as is certainly recognized by all investigators. But what is equally important and is not so generally recognized is that a measured behavior of transport, distribution, and degradation is also a performance of the biological system in which the behavior was measured. It is, however, only one possible performance--determined by environmental conditions and the state of the system--of all possible performances for which that system has the capacity. Theoretical and empirical evaluations of the capacity of a system provide the most general results we can hope to obtain for that system.

C. DESIGN OF LABORATORY ECOLOGICAL SYSTEM STUDIES IN ENVIRONMENTAL TOXICOLOGY

The immediate explanatory objective of empirical studies is to obtain sets of empirical generalizations (Fig. 1) relating to the problem and the overall defined objectives motivating the work. In the present context, the overall objectives pertain to the behavior and effects of toxic substances in ecological systems, much as we defined such objectives in the previous section. We say the immediate explanatory objective of empirical studies is to obtain *sets of empirical generalizations* because, in view of the uniqueness of capacities and environments of organismic systems, the domains of explanatory application of a particular empirical generalization based on studies of a particular ecological system cannot be large. Its application outside that domain is likely to lead to erroneous decisions. Against this probability we can protect ourselves at the empirical level of understanding only by the achieving of sets of empirical generalizations based on studies of organismic systems having different capacities and evaluated over many different sets of environmental conditions. What each such ecological system in some sense represents and how it is different from others being studied should be determined by design and results. And the design of each should make possible the elucidation of fundamentally important relationships that we can expect to exist in systems at the level of organization it is intended to represent.

The design of a laboratory ecological system amounts to the selecting or composing of an organismic system having capacities for performances of interest and to the provision of suitable and generally interesting sets of environmental conditions. When we intend to study an organismic system at the individual or population levels of organization, the problem becomes mainly one of providing suitable and generally interesting environmental conditions. This is because the potential capacity of an individual organism or a population of a given species has largely been determined by nature. Even so, we must remember that, through developmental effects of the provided environment, the realized capacities of individual organisms are in part determined by our design of laboratory ecological systems. But at the multispecies level of organization we determine not only the sets of environmental conditions but also the capacity of the system as a whole, by the species of organisms we choose to include in a laboratory ecological system. All of this we have endeavored to make clear in previous sections of this article.

Still, with all the difficulties we have considered at length, how are we to design laboratory ecological systems so as to be able to induce from observational data sets of empirical generalizations having explanatory applicability over domains sufficient to be of much value in environmental toxicology? First of all, empirical generalizations are based on general concepts of objects and relations implicitly or explicitly derived from *classification schemes*. To this we must direct much more attention. The organismic objects of concern are individual organisms, populations, and multispecies systems. For individual organisms and populations, the taxonomic classificiation of species is important, in that it in some degree reflects evolutionary similarities and differences. Classification into trophic types--autotrophic plants, herbivores, omnivores, carnivores, and decomposers--is also important, and it is necessary if we are to deal with multispecies systems. Classification of relationships among populations in multispecies systems is necessary if we are to know the domains of empirical generalizations which state general relationships between concepts of classes of objects. Examples of such relationships among organismic objects are predation, parasitism, competition, commensalism, and mutualism. Classification of physical environmental objects, relationships, and modes of operation is also necessary. F. E. J. Fry's (1947) scheme of operational classification of environmental factors--lethal, controlling, limiting, stressing, masking--should prove very useful at all levels of biological organization, especially since he developed this scheme to deal with general determination of the effects of environmental factors on the scopes for performance of organisms. And, if we are to achieve sets of empirical generalizations useful in environmental toxicology, we must develop adequate schemes of classification of toxicants according to their structure, behavior, modes of action, and effects. From classes of organismic and environmental objects and relations, we can choose representative ones to incorporate in our designed laboratory ecological systems and thus simplify the problem of empirical generalization and clarify the domains of explanatory applicability of individual and sets of empirical generalizations.

For laboratory ecological systems at the individual organism level of organization, we should select species as broadly representative of taxonomic and trophic classes as possible. And examples of a rather wide variety of these classes should be investigated. And always we should evaluate the capacities of the organisms we study by determining their scope for performance under many different sets of environmental conditions, including toxicants of different classes. Food or other energy and material availability, temperature, water availability, and other important factors in the natural environments of the species to be studied should be varied over interesting ranges in determining toxicant behavior and effects and scopes for performance of individual organisms. Even if it is not our intention to study multispecies systems, in the restricted sense we define these, it may still be worthwhile to include in the environment of the individual organism of interest individuals of other species that may alter its scope for performance. Finally, our definition of an individual organism, as an organismic system, incorporates the entire life history trajectory of the individual, from zygote through development to and including reproduction. Our empirical generalizations, as they apply to individual organisms, must relate sets of environmental conditions to sets of performances of different kinds--scopes for performance--at all life history stages. In this way, generalizations pertaining to the individual organism level will relate more nearly to generalizations pertaining to the population level of organization than they would were we to deal only with particular life history stages.

This is because a population differs from a simple aggregation of individual organisms of the same species in that it has the capacity to persist through many generations of individuals as a result of life history completion and reproduction of these individuals. Our empirical generalizatins about populations should relate effects of particular classes of toxicants to the persistence and other capacities of populations under a wide range of other environmental conditions, through determination of population scopes for performance. To do this, we must provide those environmental conditions necessary for completion of individual life histories and for the development and persistence of the resulting population. Energy and material resource levels must be adequate, but should be studied at different quantitative levels, and qualitative difference should also be tested. And, as with the individual organism, environmental factors such as temperature and water availability should be included in our evaluations of population scope for performance. In addition, without creating persistent multispecies systems, the capacities of populations can be further evaluated by including in the environment of the population different densities of the species such as competitors or predators.

Simply because it may sometimes be possible and useful to study the capacities and performances of individual organisms and populations interacting with other species that do not together form a system does not mean that this is always the best approach. *There are good reasons for evaluating capacities and performances of individual organisms and populations in what are indeed multispecies systems having capacities for persistence and other performances that the organisms and their populations separately do not possess.* And, of course, if we are interested in the behavior and effects of toxic substances in multispecies systems, then we have no choice but to study such systems, either in nature or in the laboratory. The creation of multispecies systems in the laboratory--systems having their own, level-specific, capacities to persist, develop, and provide for their population and individual organism parts--requires considerable knowledge of the biological characteristics and requirements of species considered for inclusion. Moreover, unless success in developing a multispecies system is to be achieved only by chance through an indeterminate number of trials, there must be some theoretical means of deducing from life history characteristics and parameters of candidate species the likelihood of our being able to form with them a multispecies system having the capacity to persist through many generations.

To develop a laboratory ecological system that is indeed a multispecies system, we must provide for completion of the life histories of individuals of the species included. But, for the system to have the capacity to persist, this alone is not enough. Multispecies system persistence is possible only if the capacities of the individual populations for numerical and biomass increase are great enough at each step in the energy and material transfer pathways to sustain successive steps. When this condition has not been met, multispecies systems have not been created and toxic effects of substances on a multispecies system as a whole and the behavior of the toxicant in the system cannot be reliably evaluated.

If we have indeed created a multispecies system having capacities for persistence and organization, we ought to evaluate that capacity under different sets of environmental conditions--we ought to determine the scope for performance of that system under a range of conditions of interest. This is because no particular set of environmental conditions is of general interest, and the multispecies system will have different performances, including structure, with changes in environmental conditions.

We should also note that laboratory multispecies systems are severely limited in their capacity for development, or change in structure, because "colonization" by new species is generally eliminated or severely restricted (Warren and Davis, 1971).

Finally, however fully we may be able to evaluate it, any multispecies system has its own capacity. The capacity of a multispecies system in the laboratory we determine by bringing together individual organisms of different species having their own capacities. Whatever may be this capacity for performances--including transport, biomagnification, and biodegradation of toxic substances--we have determined it by chance or by design. It is true that each of the individual organisms have certain capacities of assimilating, accumulating, and degrading toxic substances, and these capacities nature determined. But nature does not determine the capacity of any laboratory multispecies system as a whole. We ought to design laboratory multispecies systems to include representative populations and relations, including predation, competition, commensalism, and mutualism, if these systems are to behave at all like natural ones. Even then, we must continue to be aware that the capacity of any designed system is peculiar to it, and general application of laboratory results to nature should be made with great care and with the assumptions made explicit. An empirical generalization, at the multispecies level of ecological system, should make explicit the nature of the system from which it was derived. And we need such generalizations for different multispecies systems designed to include various combinations of species populations and interrelations.

D. APPLICATION OF LABORATORY ECOLOGICAL SYSTEM STUDIES IN ENVIRONMENTAL TOXICOLOGY

The goal of science--the increase in human understanding--ever must be not only relevant to and concordant with other goals of society but indeed must be one of the major goals of humanity, for creativity and the search for understanding most uniquely characterize mankind. It is not understanding but rather misuse or insufficiency of understanding that leads to human social problems. Objectives of particular scientific endeavors, even if not so relevant to specified social problems as might be supposed, ought to be formulated in ways making their pursuit likely to contribute to understanding and so to society. Redefinition of either social or scientific problems so as to make possible their solution is not simply an artifact of science: Defining problems in ways that the world can be understood is the essence of science. We must not take too narrow a view of what is or is not relevant to any human concern, including problems in the domain of environmental toxicology.

Human capacities may demand some narrowness of definition of social and scientific problems and objectives for any single institutional means of approach to be employed. But we must endeavor to avoid the narrowness of view that vitiates our efforts. Society through its scientific and other institutions may at any time seem to demand of us narrow views and approaches intended to solve social and scientific problems. Perhaps this is inevitable and even apparently necessary in the short run, but its social and scientific consequences have too often been found to be inconsequential in the long run. Social and natural scientists owe it to themselves and to society to take broad views, and they have the responsibility of teaching the necessity of this.

The objectives of laboratory ecological system research, as they appear at the bottom of Figure 30 and as articulated in Figure 31, appear to be relevant to scientific problems in environmental toxicology. And their achievement would presumably be useful in solutions of technological, governmental, and educational problems also necessary to solution of the social problems facing us. Beginning at the top of Figure 30, we have attempted to delineate, through successive decomposition of problems finally to problems at ecological levels of organization, a pathway through which the relevance of the objectives of laboratory ecological system research might be informally evaluated. Even though this delineation is in no way comprehensive, it does make apparent that most of the objectives of laboratory ecological system research can be approached in other ways and that their realization, by whatever theoretical or empirical means, can only very partially resolve pertinent problems in the biological sciences and must be accompanied by solution of problems in the social and physical sciences in order to contribute importantly to solution of technological, governmental, and educational problems and the social problem itself. This conclusion must be obvious to all concerned, but nevertheless should be noted in a consideration of the relevance of the objectives of any scientific approach to complex social problems such as those occurring in the domain of environmental toxicology.

Our problem lies not with such superficial relevance of defined objectives but with how even defined objectives are perceived and understood differently by various scientists, for it is the way in which objectives are understood that determines how they are pursued and the relevance of accomplished scientific work to social problems. It is here, to speak only of the domain of biology, that matters of how the biological world is to be perceived and understood become so important. For one view of the biological world will lead to very different interpretation and pursuit of even carefully defined objectives than will another, and these will lead to different relevances of the work to scientific and social problems. It is for this reason that we considered the nature of natural ecological systems, as seems apparent to us, in Section II of this article. And there we went so far as to articulate an abstract conceptual framework for biology and to interpret it at ecological levels of organization. We will not here argue whatever adequacy this view of the biological world and ecological systems may or may not have. Here, it is only important that the basis for judgments we make as to the meaning of defined objectives and their relevance to solutions of problems in environmental toxicology has been made explicit, so that those concerned can evaluate the rationality of those judgments based on our presuppositions. We judge the levels of organization actually represented by laboratory ecological systems and the capacities of the representational models to underlie possible interpretation of defined objectives and thus to underlie the relevance of these objectives and work done in their pursuit to problems in environmental toxicology.

Let us first consider what levels of biological organization the models being called laboratory ecosystems may represent. If, say six or seven species representing the major trophic kinds--plants, herbivores, omnivores, carnivores, and decomposers--are indeed so adapted to one another and to the system as a whole that this whole has its own system capacities, what level of natural organization may we suppose this laboratory ecosystem represents? Some *a priori* view of the nature of natural ecosystems is necessary to respond to this question. If, for purposes of argument, one accepts our view of the organization of natural ecosystems, then what some of us have been calling laboratory ecosystems represent--in terms of dimensions and also in terms of capacities--at most very low levels of ecosystem organization. This must have something to do with the capacities, the performances, and what we can conclude about intoxication of natural ecosystems, on the basis of laboratory ecosystem studies. This is so no matter what our particular objectives may be--evaluation of relative toxicity, evaluation of ecological magnification and biological degradation of toxicants, or determination of toxic effects on individuals, populations, and communities. The term *ecosystem*, as employed in ecology, has generally meant a natural biological community together with its physical and chemical environment. No one supposes laboratory ecosystems have either the dimension or the capacities of natural ecosystems. But we must be careful not to attribute directly to natural ecosystems the capacities and performances of laboratory ecosystems, use of the term laboratory ecosystem perhaps suggesting more relevance than we have any reason to assume.

Now, of course, laboratory models, just as theories, are representational idealizations intended to aid our search for understanding of nature. Good models, just as good theories, must not simply reflect nature in all the dimensions of her complexity but must somehow represent that which is most important in determining the behavior of natural systems. It is not the reduction of dimensions of laboratory ecosystems that may vitiate their use in environmental toxicology, but whether dimensions have been reduced in such a way as to leave the models representing nothing at all of importance in natural ecosystems. It is the capacity of a system that determines the environments in which it could possibly persist and what its performances can possibly be in any particular environment. High level systems have their own level-specific capacities determined in part by the capacities of their subsystems (Fig. 4). *More than anything else, our laboratory ecosystems must be designed so as to possess capacities representative of capacities of low-level subsystems of natural ecosystems; in no way can they represent the capacities of natural ecosystems as wholes. But if we can demonstrate that even low level systems have capacities for ecological magnification and biological degradation and that* *capacities for persistence or production are decreased by toxic actions, it is conceptually and theoretically sound to conclude that the capacities of natural ecosystems will entail such capacities and alterations of capacities of their lower-level subsystems.* The distinction between capacity and performance of systems here becomes of the greatest importance for although there is general interest in the capacities of laboratory multispecies systems, there is little general interest in their particular performances. This is because not only the capacities but the environments of laboratory multispecies systems are different from those in nature, and there is no reason to suppose that magnitudes of particular performances determined in the laboratory correctly reflect magnitudes of the performances in nature. For these reasons, we have placed great emphasis on the capacities of individual organisms, populations, and multispecies systems in the interpretation of objectives for laboratory ecosystem research in environmental toxicology (Fig. 31). Understood in this way, we believe these objectives to be quite relevant to problems in environmental toxicology.

But application of results of laboratory ecological system studies to the solution of problems in environmental toxicology cannot be direct or simple, for the relationships between knowledge obtained in the laboratory and the nature of the natural systems in which we perceive problems are indirect and complex. For this reason, in the previous section we emphasized our view that the immediate explanatory objective of laboratory ecological system studies should be development of sets of empirical generalizations. Particular generalizations, based on the results of laboratory ecological system studies of particular designs, should state as generally as possible the behavior and effects of representative toxicants in such laboratory systems. But the generalizations must in some way specify the nature of the laboratory model yielding the results from which the generalizations were induced. This must be done because of the uniqueness of a particular laboratory ecological system. To deal with the problem of such uniqueness, and thus with the problem of limited generality of particular generalizations, we must study many different kinds of laboratory ecological systems. We must, of course, study laboratory systems having different levels of biological organization: individual organism, population, and multispecies systems. But, even at each general level of organization, different species, relations, and environmental conditions must be investigated. Perhaps some few generalizations will pertain to all such systems, and these will be extremely valuable. But many important generalizations may not apply to all the systems studied and some generalizations superficially are likely to appear to be contradictory. Such an appearance may be owing only to inadequacies of our conceptual and theoretical framework. Generalizations relating directly to one level of biological organization will not generally be adequate for direct application to other levels of organization. Nevertheless, because of the hierarchical organization of multispecies systems into population and individual level subsystems, we may be able to see ways of ordering empirical generalizations pertaining to the different levels of organization so as to represent multispecies systems and behavior and effects of toxicants more adequately. This may best be achieved with scientific deductive systems. But adequate scientific deductive systems are extremely difficult to create. And some more or less rational and useful way of ordering empirical generalizations, short of a formal deductive system, may be attainable.

Of course, if we do achieve a theory making possible the deduction of sets of empirical generalizations, we have made an important advance in science and its application to solution of problems in environmental toxicology. Such a theory makes possible the explanation and logical unification of the different generalizations, even ones that might otherwise appear contradictory. Then we can see the relationships among the generalizations and the boundaries of explanatory applicability of any one of them. And the entire deductive explanatory system covers a much broader domain of nature and environmental problems there occurring. Moreover, especially if the theory is encompassed by an explicated conceptual framework, we can more clearly see the assumptions we make when we apply any part of the theory, including the deduced empirical generalizations, to solution of problems in environmental toxicology.

Finally, it is our strong feeling that we ought not to expect from biological theories, models, and empirical generalizations much in the way of quantitative prediction of the behavior and effects of toxicants in natural ecological systems. Certainly our laboratory ecological systems must generally leave out too much for this to be possible. And empirical generalizations derived from study of such systems can add nothing more. Theories do add something more. But the unique capacities and various environments of organismic systems lead to such vast arrays of kinds and levels of performances that we are not likely to soon have theoretical or other ways for achieving precise quantitative prediction. Rather, we think, it is the kinds of relationships and the forms of relationships among biological identities and the sorts of changes in these resulting from toxicants with which we can hope to deal by theoretical and empirical means. It is this sort of "qualitative," rather than strictly quantitative, application of the results of laboratory ecological system studies that we can reasonably expect to be successful.

REFERENCES

1. Andrewartha, H. G., and L. C. Birch. The Distribution and Abundance of Animals. The University of Chicago Press, Chicago. 1954.

2. Bertalanffy, L. von. General System Theory: Foundations, Development, Applications. George Braziller, New York. 1968.

3. Bisson, P. A., and G. E. Davis. Production of Juvenile Chinook Salmon, *Oncorhynchus tshawytscha*, in a heated model stream. Fish. Bull. 74 (4):763:774. 1976.

4. Booty, W. M., and C. E. Warren. A General Theory of Productivity and Resource Utilization. Manuscript.

5. Braithwaite, R. B. Scientific Explanation: A Study of the Function of Theory, Probability, and Law in Science. Cambridge University Press, London. 1953.

6. Braithwaite, R. B. Models in the Empirical Sciences. *in*: Nagel, E. et al. (eds.). Proceedings of the Congress International Union fo Logic, Method, and Philosophy of Science. 1960.

7. Carson, R. Silent Spring. Houghton Mifflin Company, Boston. 1962.

8. Clements, F. E. Plant Succession. Carnegie Institute of Washington Publication 242, Washington. 1916.

9. Cole, L. K., J. R. Sanborn, and R. L. Metcalf. Inhibition of Corn Growth by Aldrin and the Insecticide's Fate in the Soil, Air, Crop, and Wildlife of a Terrestrial Model Ecosystem. Environmental Entomology 5:583-589. 1976.

10. Fry, F. E. J. Effects of the Environment on Animal Activity. University of Toronto Studies Biological Series 55, Ontario Fisheries Research Laboratory Publication 68. 1947.

11. Gleason, H. A. The Structure and Development of the Plant Association. Bulletin of Torrey Botanical Club 44:413-481. 1917.

12. Gleason, H. A. The Individualistic Concept of the Plant Association. Bulletin of the Torrey Botanical Club 53:7-26. 1926.

13. Gillett, J. W. and Jay D. Gile. Progress and Status Report on Terrestrial In-house System. Proceedings of "Substitute Chemicals Program - The First Year of Progress." 1975.

14. Gutting, G. Conceptual Structures and Scientific Change. Studies in History and Philosophy of Science 4:209-230. 1973.

15. Hanson, N. R. Patterns of Discovery. Cambridge University Press, Cambridge. 1958.

16. Isensee, A. R. and G. E. Jones. Distribution of 2,3,7,8-tetrachlorodibenzo-p-dioxin (TCDD) in Aquatic Model Ecosystem. Environmental Science and Technology 9:668-672. 1975.

17. Isensee, A. R., P. C. Kearney, E. A. Woolson, G. E. Jones, and V. P. Williams. Distribution of Alkyl Arsenicals in Model Ecosystem. Environmental Science and Technology 7:841-845. 1973.

18. Kanazawa, J., A. R. Isensee, and P. C. Kearney. Distribution of Carbaryl and 3,5-xylyl Methylcarbamate in an Aquatic Model Ecosystem. Journal Agricultural Food Chemistry 23:760-763. 1975.

19. Kuhn, T. The Structure of Scientific Revolutions. University of Chicago Press, Chicago. 1962.

20. Lewontin, R. C. The Genetic Basis of Evolutionary Change. Columbia University Press, New York. 1974.

21. Liss, W. J. The Dynamics of Exploited Fish Populations Exposed to Dieldrin. MS Thesis. Oregon State University. 1974. 73 pp.

22. Liss, W. J., and C. E. Warren. On the Possible Form of Future Fisheries Theory. Manuscript.

23. Lloyd, R. The Toxicity of Zinc Sulfate to Rainbow Trout. Annals of Applied Biology 49:535-538. 1960.

24. Lu, P-Y., R. L. Metcalf, A. S. Hirwe, and J. W. Williams. Evaluation of Environmental Distribution and Fate of Hexachlorocyclopentadiene, Chlordene, Heptachlor, and Heptachlor Epoxide in a Laboratory Model Ecosystem. Journal Agricultural Food Chemistry 23(5);967-973. 1975.

25. Maguire, B. Jr. Niche Response Structure and the Analytical Potentials of its Relationship to the Habitat. American Naturalist 107:213-246. 1973.

26. Matsumura, F., and H. J. Benezet. Studies on the Bioaccumulation and Microbial Degradation of 2,3,7,8-tetrachlorodibenzo-p-dioxin. Environmental Health Perspectives 5:253-258. 1973.

27. Metcalf, R. L. Screening Compounds for Early Warnings about Environmental Pollution. Proc. Univ. Mo. Annual Conf. Trace Subst. Environ. Health 8:213-217. 1974a.

28. Metcalf, R. L. A Laboratory Model Ecosystem to Evaluate Compounds Producing Biological Magnification. Pages 17-38. *In* W. J. Hayes, Jr. (Ed.), Essays in Toxicology, Vol. 5. Academic Press, New York. xii + 189 pp. 1974b.

29. Metcalf, R. L. A Laboratory Model Ecosystem for Evaluating the Chemical and Biological Behavior of Radio-labelled Micro-pollutants. Pages 49-63. *In* E. R. A. Beck (Ed.) Comparative Studies of Food and Environmental Contamination. Proceedings International Atomic Energy Agency Series. 1974c.

30. Metcalf, R. L., I. P. Kapoor, P-Y. Lu, C. K. Schuth, and P. Sherman. Ecosystem Studies of the Environmental Fate of 6 Organo Chlorine Pesticides. Environmental Health Perspectives 4:35-44. 1973.

31. Metcalf, R. L. and J. R. Sanborn. Pesticides and Environmental Quality in Illinois. Illinois Natural History Survey Bulletin 31:381-436. 1975.

32. Metcalf, R. L., G. K. Sangha and I. P. Kapoor. Model Ecosystem for the Evaluation of Pesticide Biodegradability and Ecological Magnification. Environmental Science and Technology 5:709-713. 1971.

33. Morgan, J. P. Effects of Aroclor 1242^R (a Polychlorinated Biphynl) and DDT on Cultures of an Alga, Protozoan, Daphnid, Ostracod, and Guppy. Bulletin Environmental Contamination and Toxicology 8:129-137. 1972.

34. Mount, D. I., and C. E. Stephan. A Method for Establishing Acceptable Toxicant Limits for Fish -- Malathion and the Butoxyethanol Ester of 2,4-D. Transactions of the American Fisheries Society 96:185-193. 1968.

35. Nagel, E. The Structure of Science. Harcourt, Brace, and World, New York. 1961.

36. Popper, K. The Logic of Scientific Discovery. Basic Books, New York. 1959.

37. Ramensky, L. G. Die Grundgesetzmassigkeiten im Aufbau der Vegetationsdecke. Wjenstn. opytn. djela Woronesch. (Bot. Centralbl., N. F. 7:453-455). 37 pp. 1924.

38. Roelofs, T. D. Effects of Dieldrin on the Intrinsic Rate of Increase of the guppy, *Poecilia reticulata* Peters. Ph.D. Thesis Oregon State University, Corvallis. 1971.

39. Sanborn, J. R., and C-C. Yu. The Fate of Dieldrin in a Model Ecosystem. Bulletin Environmental Contamination and Toxicology 10:340-346. 1973.

40. Seim, W. K., J. Lichatowich, R. Ellis, and G. Davis. Effects of Kraft Mill Effluents on Juvenile Salmon Production in Laboratory Streams. Water Research 11(2):189-196. 1977.

41. Shumway, D. L., C. E. Warren, and P. Doudoroff. Influence of Oxygen Concentration and Water Movement on the Growth of Steelhead Trout and Coho Salmon Embryos. Transactions of the American Fisheries Society 93:342-356. 1964.

42. Silliman, R. P. Interaction of Food Level and Exploitation in Experimental Fish Populations. Fisheries Bulletin of Fish and Wildlife Service 66:425-439. 1968.

43. Taub, F. B. Biological Models of Freshwater Communities. EPA-660/3-73-008. 1973.

44. Thatcher, T. O. Some Effects of Dissolved Oxygen Concentration on Feeding, Growth and Bioenergetics of Juvenile Coho Salmon. Ph.D. Thesis, Oregon State University, Corvallis. 1975.

45. Toulmin, S. Philosophy of Science. Harper and Row, New York. 1960.

46. Warren, C. E. Biology and Water Pollution Control. W. B. Saunders, Philadelphia. 1971.

47. Warren, C. E., W. K. Seim, R. O. Blosser, A. L. Caron, and E. L. Owens. Effect of Kraft Effluent on the Growth and Production of Salmonid Fish. Tappi 57(2):127-132. 1974.

48. Warren, C. E., M. W. Allen, and J. H. Haefner. Conceptual Frameworks for Biology: A Tentative Proposal. Manuscript.

49. Warren, C. E., and G. E. Davis. Laboratory Studies on the Feeding, Bioenergetics, and Growth of Fishes. *In* S. D. Gerking (ed.), The Biological Basis of Fish Production. Blackwell Scientific Publications, Oxford. 1967.

50. Warren, C. E., and G. E. Davis. Laboratory Stream Research: Objectives, Possibilities, and Constraints. Annual Review of Ecology and Systematics 2:111-144. 1971.

51. Wurtsbaugh, W. A. Effects of Temperature, Ration, and Size on the Growth of Juvenile Steelhead Trout, *Salmo gairdneri*. MS Thesis, Oregon State University, Corvallis. 1973.